THE PREDICTORS AND CONSEQUENCES OF INDIVIDUAL VARIATION IN SOCIALITY IN BLACK-TAILED PRAIRIE DOGS (*CYNOMYS LUDOVICIANUS*)

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ABSTRACT

Sociality describes the organization of members of a species in a group to maximize fitness. It is thought to evolve when the benefits of existing in social groups outweigh the costs. Typically, these costs and benefits are generalized to the species or population level and not at the level of the individual, where the decisions and the consequences of those decisions regarding sociality often resides. Social network analysis (SNA) provides a tool to test hypotheses to identify variation in sociality at an individual level, as well as the potential trade-offs associated with this variation in sociality, which may change across time. In many SNA studies, the temporal variation of the cost/benefit structure is often ignored. Black-tailed prairie dogs (*Cynomys ludovicianus*) live in highly social colonies and display an elaborate range of social behaviours. Previous research had indicated that individuals live in sub-community structures called coteries, containing one breeding male and a harem of females. The social structure of this species dramatically shifts during the reproductive period. As prairie dogs have this shift in sociality, it is the best time to investigate these potential trade-offs. I constructed social networks of members of a prairie dog colony from the northern limit of their range, in southern Saskatchewan through behavioural observation and examined correlates of variation in sociality between and within individuals (across time). I compared sociality between two seasons that greatly differed in their importance for reproductive success. I determined that better body condition enabled individuals to maintain social stability over time. Furthermore, individual prairie dogs vary their level of sociality over the year, presumably to optimise individual fitness. Reproductive females decrease their sociality during the breeding period to maximize foraging time and availability for defense of their litter, while reproductive males increase their aggressive interactions to defend the home range and resources their coterie females require for foraging. I found that females that maintained affiliative social connections within their own coterie had higher reproductive success than those connecting adjacent coteries, while variation in frequency of agonistic connections did not correlate with reproductive success. This research improves the understanding of the utility of SNA for wild populations through examining acute behavioural shifts and using new temporal methodologies previously unused in wild populations.

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DEDICATION

Charlie Bailey,
for keeping me going when it mattered most,
&
my endlessly supportive parents,
Lynn and Agnes,
who refused to waver in their belief in my ideas and my strength.

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CHAPTER 1:

GENERAL INTRODUCTION

1.1 Sociality

Sociality is described as the tendency for individuals of a species to associate together and cooperate (Krause and Ruxton 2002). There are several hypotheses that support the evolution of sociality, but all are resultant in increased fitness under particular ecological pressures (Wrangham 1986). These hypotheses are: (1) predator avoidance, (2) resource distribution, and (3) mate availability (Wrangham and Rubenstein 1986, Wrangham 1986). Firstly, a given individual's risk of predation decreases as group size increases. There are two primary reasons contributing to this association: one, predators are less likely to approach a large group than a small one (confusion effect); and two, the likelihood of a particular individual being preyed upon decreases with a larger number of nearby conspecifics (dilution effect) (Krebs and Davies 1997). Secondly, the distribution of resources on the landscape may drive individuals of a species to frequent the same areas by selecting for resources at a higher rate than present on the landscape leading to individuals existing in groups based on these resource patches. Thirdly, Wrangham (1986) provided evidence that mammal sociality evolved from females forming groups. This philopatry creates opportunities for males to aggregate near female groups, providing increased mate availability and choice. Each of these hypotheses results in increased fitness through increased survival and reproductive success, despite the associated costs. The balance of costs and benefits of sociality for species may differ based on life history or morphology, resulting in a wide range of social groups.

Animal species occur on a spectrum of social organization that ranges from solitary individuals to long-term maintenance of eusocial groups (David-Barrett and Dunbar 2013, Nowak et al. 2010). The traits that organize species on this spectrum are: (1) parental investment, (2) cohabitation between adults and offspring, (3) cooperative care of young, (4) division of labour, (5) caste system, and (6) overlapping adult generations (Krause and Ruxton 2002). Examples of well-studied social systems include eusocial insects of Hymenoptera (Nowak et al. 2010), family groups in Cetacea, (Lusseau 2003), and advanced societies in Primates (Mitani et al. 2012). This spectrum of sociality is often influenced by the arrangement of social groups: age, sex, body size, kinship, as well as spatial and temporal arrangement are common factors

influencing the sociality of a species. These factors can be found to segregate populations based on phenotypic matching or hierarchical systems.

The formation of social bonds between individuals has been suggested to be highly influenced by age, as with increasing age, new social developments occur. In some instances, young individuals are found to be the most influential in group transitivity (Ramos-Fernandez et al. 2009), while others have suggested that older individuals maintain the social hierarchy (Mitani et al. 2012). Further, in other systems, age groups appear to segregate. For example, harbor seals (*Phoca vitulina*) haul out by age class with adult females segregating from sub-adults (Kovacs et al. 1990). Similarly, yearling male macaques (*Macaca mulatta*) self-segregate from other sex and age classes (Hassett et al. 2010).

In most of these cases, age and sex are inter-related in attributing social rank or segregation. Primate societies, for example, are typically matrilineal, with older females maintaining the highest ranks in a group (Mitani et al. 2012). However, these two traits can also be independent. Male merino sheep (*Ovis aries*) consistently choose to associate with other males regardless of age, when choosing between female and male herd members of the same proximity (Michelina et al. 2005). A recent study by McDonald and Pizzari (2018) suggest that observed sexual selection strategies (polygynous, monogamous, polyandrous) are particularly influenced by the sexual assortment of the population.

Social rankings are also commonly determined by body size or body condition. Sexual dimorphism due to sexual selection, in many taxa, has often resulted in larger males in better body condition that compete for a harem of females in polygynous groupings or the adaptation of different breeding strategies based on body size (Shine 1989). Body size is also a contributing factor to segregation in other species. Similar sized fish will shoal together to reduce phenotypic oddity, which is advantageous as predators would not be able to distinguish easy prey based on body size (Hoare et al. 2000). These examples illustrate the complexities of body size and sociality relationships: choosing to associate with individuals of similar size is beneficial for anti-predator strategies but separating from similar size can be advantageous for sexual selection purposes.

Across multiple taxa, philopatry of the natal group has resulted in social groups across taxa. Individuals that share kinship are more likely to associate with each other than unrelated

individuals likely due to indirect fitness benefits or familiarity (Emlen 1994). This is particularly true in many rodent species, resulting in large cooperative social groups. Females of great gerbils (*Rhombomys opimus*) were more genetically similar within their groups than outside of the group and share resources within the shared kinship (Randall et al. 2005). Columbian ground squirrels (*Urocitellus columbianus*) exhibit few aggressive interactions to kin, and the number of aggressive interactions received decreases with age, where individuals have settled into their higher dominant rank (Viblanc et al. 2016). One common phenomenon of natal philopatry is matrilineal rank inheritance (Kawamura 1958). Females are likely to inherit their mother's social rank based on remaining in the natal group, which inherently also increases the level of kinship within the group, promoting further cooperation.

Social groups are highly linked to philopatry and preferential resource locations, as individuals associate on the landscape based on these familiar natal territories or resource abundance. The spatial arrangement of individuals, as well, is highly linked to the above factors (i.e. age, sex, body size, and kinship), as many of the choices based on these other factors are reinforced by already encountering and sharing the same space. Some species maintain home range for their entire lives, connecting the social and spatial landscape (Verdolin et al. 2014, Viblanc et al. 2016), while resource selection underlines social groupings in migratory species (Webb et al. 2010).

In order to best exploit conditions for individual fitness, individuals of certain phenotypes may alter their social arrangement over time. Female macaques vary their social behaviours during the mating and birthing seasons by increasing the amount of time they spend being social and the number of individuals they are social with during the mating season (Brent et al. 2013). Oh and Badyaev (2010) found that male house finches (*Haemorhous mexicanus*) are able to increase their own attractiveness (and therefore, fitness) by decreasing the number and types of network connections during the breeding season.

1.2 Trade-offs of sociality

Social living with conspecifics offers a range of costs and benefits that are common across many taxa (Krause and Ruxton 2002, Kutsukake 2009). The most commonly cited benefit of sociality is protection against predation, as this is considered a primary driver of social evolution as discussed above. Along with the dilution and confusion effects, living in a group also allows

for increased vigilance of predators and faster transfer of information (Krause and Ruxton 2002). Anti-predator benefits are observed in social behaviours like shoaling (fish), flocking (birds), and herding (mammals). A second benefit of social living found across taxa is increased reproductive success. Species that form crèches use cooperative care of offspring to increase survival of offspring from many parents (Packer et al. 2001). By receiving parental investment from additional adults, the chance of survival in offspring increases (Packer et al. 2001). This is a behaviour commonly found in many bird species but is also found in mammal species including lions (*Panthera leo*, Packer et al. 2001). Other species-specific benefits include increased opportunity of mate choice (Westneat et al. 2000), increased foraging success (Kutsukake 2009), and thermoregulation (Blumstein et al. 2004). Despite the range of benefits, there are also a number of costs associated with group living, of which intra-specific competition, increased frequency of aggressive interactions, increased transmission of infection and parasites, and delayed reproduction are the most common (Krause and Ruxton 2002, Silk 2007). While these costs and benefits are observed and studied at the population level, these benefits only exist upon individuals' decisions to maintain these groups through balancing their own costs and benefits of group membership.

1.3 Social network analysis

Social network analysis (SNA) interprets and illustrates interactions within a social group (Croft et al. 2008). Social network analysis has been employed within the social sciences for decades (Moreno 1934, Lewin 1951); however, its use for deciphering behavioural interactions in non-human animals is more recent (Sutherland 1996, Krause and Ruxton 2002). Social network analysis uses a system of 'nodes' and 'edges' to represent behavioural interactions as connections between individuals within a population (Figure 1.1; Croft et al. 2008). A node represents the individual within the network, while the edge represents the interactions between the nodes. Historically, individuals within a population were treated as having an equal likelihood of interacting with all others (Maynard-Smith 1982). In other words, all nodes have an equivalent number of edges in a population. However, in most animal systems, this is not the case. For example, the transfer of information of predator awareness is most effectively conveyed to those central to a network. In Figure 1.1, if information was received at node 1 and shared through the population, then node 3 could receive this information from nodes 2, 4, and 5,

and is therefore the most likely to benefit. In contrast, nodes 6, 7, 8, 9, and 10 can only receive information through node 3. This impairs their ability to respond appropriately to a potential predator threat and therefore, may decrease their chance of survival relative to others.

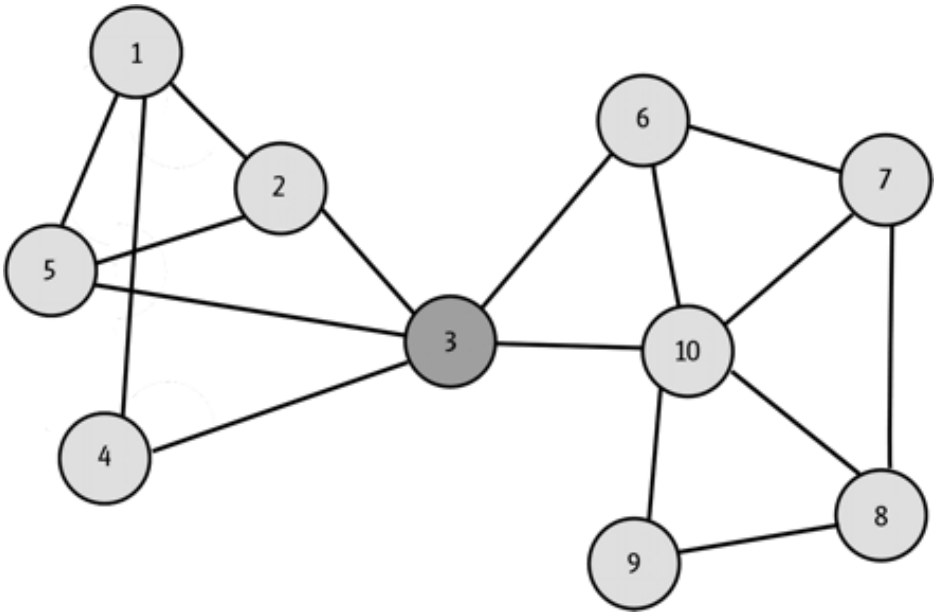

Figure 1.1. A simplistic example of a social network with 10 nodes (represented by the grey circles) and the edges (black lines) representing the connections between the nodes (adapted from Coleing 2009). Node 3 is deemed most central as it has the most edges, but also connects two subgroups that otherwise would not be connected (measured as betweenness centrality which is further discussed in the statistical analysis portion of the methodology).

Despite their wide range of social systems (Michener 1983), rodent populations have been underrepresented in SNA to date (Croft et al. 2008; Krause et al. 2015), In this thesis, I will explore the utility of SNA for understanding the complicated social relationships of one social rodent: black-tailed prairie dogs (*Cynomys ludovicianus*). One of the current limits on the field of SNA is the small range of behaviours that have been used to create the networks (Krause et al. 2015). In cetaceans and ungulates, for example, association data using GPS loggers or 'gambit of the group' methodologies are used to provide the basal image, but real inferences cannot be made on the types of behaviours that modify the network as it cannot be determined if the interaction is affiliative or agonistic (Franks et al. 2010, Krause et al. 2015). In this regard,

social rodents, such as prairie dog species are of interest to SNA due to their highly visible and variable social behaviours (King 1955, Slobodchikoff et al. 2009). Additionally, these populations display high site fidelity and are relatively sedentary, where individuals of the network are easily followed and changes in the network should be highly apparent (Verdolin et al. 2014). Verdolin et al. (2014) has suggested that prairie dogs provide ideal systems to describe substructures and hierarchical organization in social networks. Social network analysis can be used to tease apart individual and population variation but is also useful for finding sub-group variation, which is valuable in addressing the impact of sociality on individual fitness.

1.4 Study species

Black-tailed prairie dogs (*Cynomys ludovicianus*, hereafter 'prairie dogs') are small (< 2kg) colonial mammals found on prairie habitats spanning from southern Canada through to northern Mexico. Prairie dogs within a colony are grouped into coteries of related individuals (Hoogland 1995). A coterie is a polygynous unit typically containing one dominant male, several adult females, as well as yearlings and juveniles of both sexes (Hoogland 1995). This coterie structure allows for complex social groupings with dynamic and distinct social interactions. It is unknown how these social interactions and their possible variation across individuals influences individual survival and success.

The prairie dog social system is considered highly complex due to their advanced social behaviours and interactions (Slobodchikoff et al. 2009). These behaviours include both affiliative and agonistic encounters. The affiliative behaviours include allogrooming, anal sniffing, alarm calling, greet-kissing, and jump-yipping (King 1955, Hoogland 1995). Some of these behaviours are fairly well understood, while some require more explanation as there still remains some debate as to the purpose of these behaviours. Grooming and calling are used as altruistic strategies to lower parasite load in nearby individuals and to increase information transfer of predator awareness to increase survival, respectively. Lowering parasite load is of particular importance in this species as the sylvatic plague, carried by species of flea commonly found on prairie dogs, is linked to 99% mortality in infected colonies (Cully and Williams 2001). Greet-kissing involves prairie dogs opening their mouths, locking teeth, and touching tongues (King 1959). Steiner (1974, 1975) has proposed three hypotheses to describe the purpose: (1) food information hypothesis (to infer the resources recently collected by nearby conspecifics), (2)

individual recognition hypothesis (to identify conspecifics and potential unfamiliar dispersers), and (3) dominance maintenance hypothesis (to reinforce hierarchies amongst coteries). Regardless, it is suspected that greet-kisses allow for maintenance of social affiliation, despite the presence of multiple hypotheses (Slobodchikoff et al. 2009). Jump yipping describes when a prairie dog lifts its body into a vertical jump with forelimbs extended above the head, while letting out a sharp bark (Smith et al. 1976). Initially this was interpreted as a territory defense display (King 1955), however, it has now been shown to demonstrate a contagious display of social awareness (Hare et al. 2014) and to signal the 'all clear' in a coterie (Smith et al. 1976). Prairie dogs often sniff other individuals to identify familiar and unknown individuals, which typically continues to further affiliative behaviours, but can sometimes escalate to agonistic responses. Agonistic behaviours include territorial defense, fighting, and chasing (Hoogland 1995). These behaviours range from fairly passive encounters to active actions, depending on the intensity and frequency of the behaviour. Choosing one interaction over another may reveal some insight into potential time and energy costs of social activity.

The Canadian population of prairie dogs is limited to 19 colonies located in and around Grasslands National Park, Saskatchewan (Tuckwell and Everest 2009), and is considered threatened due to isolation from its southern neighbours in Montana and declining population size (COSEWIC 2011). It is currently unknown to what degree sociality affects the survival of black-tailed prairie dogs (COSEWIC 2011). The Canadian population of prairie dogs occurs on the edge of their overall geographic range. Populations located on the edge of a geographic range are often subject to more dynamic changes in population size (Channell and Lomolino 2000), challenging weather conditions (Angert 2006), and overall lower densities (Gaston 2009) in addition to typically being isolated from other populations (Channell and Lomolino 2000, Gaston 2009). Stephens (2012) has demonstrated that the Canadian population exhibits dramatic fluctuations in population size, indicating there is great opportunity to investigate how this population may be impacted by behavioural variation.

1.5 Purpose and objectives

The purpose of my study was to examine the relationship between individual variation in sociality and individual condition, survival and reproductive success in a population of black-tailed prairie dogs located on the edge of their geographic range. My specific objectives were to:

1. examine the social relationships of prairie dogs by creating social networks for a sub-section of a colony
2. examine the variation of social interactions between individuals within the same time scale, and also the variation of sociality within an individual over time
3. investigate the factors that can predict this variation in social strategy
4. determine what components (reproductive success and ultimately, survival) may be influenced by individual variation in sociality

1.6 Thesis structure

My thesis is divided into four chapters. **Chapter 1: General Introduction** (above) covers information that illustrates details of the specific questions I will answer. **Chapter 2: Multi-level and temporal network analysis of sociality in black-tailed prairie dogs (*Cynomys ludovicianus*)** addresses my first three objectives through examining the network level correlations of social, spatial, and familial networks, and the factors that may predict changes in these networks. This chapter seeks to provide evidence that social structures supersede the spatial arrangement of each prairie dog and its neighbours. The results of this chapter explore new areas of social network analysis as a measure of within individual variation. **Chapter 3: Fitness consequences of individual variation in levels of sociality in black-tailed prairie dogs (*Cynomys ludovicianus*)** addresses the potential fitness outcomes of individual variation in sociality through reproductive success and loss from the network. This chapter specifically addresses the trade-offs associated with sociality for this species. **Chapter 4: General Discussion** provides a synthesis of both data chapters and explores the future directions and applications of this research.

CHAPTER 2:

MULTI-LEVEL AND TEMPORAL NETWORK ANALYSIS OF SOCIALITY IN BLACK-TAILED PRAIRIE DOGS (*CYNOMYS LUDOVICIANUS*)

2.1 Introduction

Sociality is described as the tendency for individuals of a species to associate together based on social attraction; specifically, interacting with conspecifics based on the benefits of social interaction and not only proximity based on resource selection (Krause and Ruxton 2002). Animal species occur on a spectrum of social organization that ranges from solitary individuals to long-term maintenance of eusocial groups based on varying trade-offs associated with group dynamics (David-Barrett and Dunbar 2013, Nowak et al. 2010). This variation is presumed due to different cost/benefit structures for different environments and species (Krause and Ruxton 2002). For example, eusocial species have highly successful colonies due to division of labour, but most individuals are sterile, thereby giving up any direct fitness benefits (Michener 1969). Conversely, communal breeding species may increase their own reproductive success by collectively caring for offspring, but this may come at the cost of infanticide or competition during extreme climate events (e.g., drought, Packer et al. 2001). For sociality to evolve, the benefits of continuously living in a group must outweigh the costs.

Traditionally, sociality was interpreted as equally likely between all individuals across the landscape (Maynard-Smith 1982). However, sociality arises from individuals within a group seeking to optimize their own cost-benefit balance and ultimately fitness. Therefore, to truly understand the evolution of sociality, we need to concentrate our efforts on the individuals that make up the group. Some attempts have been made to analyze the impact of sociality on fitness at the individual level, with the primary focus being on the spatial variation between individuals in a social group (Parrish and Hamner 1997). This variation in sociality over spatial arrangement indicates there are fitness trade-offs due to social behaviours. To understand the impact of costs and benefits of sociality to an individual's fitness, it is necessary to assess the social interactions between those individuals.

The complexities and intricacies of social groupings within the animal kingdom have drawn an increasing amount of attention due to new tools for its analysis. Social network analysis (SNA), once restricted to social sciences, has expanded into biological studies, and can investigate how the variation in behaviours among individuals affects the social structure in the population as well as individual fitness (Croft et al. 2008). Social network analysis has been used to study foraging behaviour (Adler and Gordon 1992), disease transmission (Godfrey 2013), and mate choice (McDonald et al. 2013). Typically, social networks are constructed by recording affiliative interactions, thus displaying the benefits of being social in a group or are constructed using proximity-based data that provides zero to little context of the behaviour. An example of an affiliative interaction is the grooming of a dominant individual by a lower-ranked individual as it helps to reinforce social bonds and organization (Sade 1972). However, networks can also be built using agonistic interactions, where hierarchies built on aggressive behaviour within a group can be denoted. An agonistic interaction could be chasing of one individual by another to reinforce territory boundaries (Sholtis et al. 2015). In order to fully understand the costs and benefits of being social, both affiliative and agonistic interactions must be considered as both contribute to the balance of trade-offs.

Moreover, costs and benefits are likely to vary temporally, which could potentially lead to changing group dynamics over time. Seasonal environmental shifts and life history transitions can result in the benefits of group living outweighing the costs at one point (i.e. during migration (Voelkl et al. 2015), hibernation (White and Lasiewski 1971), and reproduction (Cockrum 1969)), while at others, the cost/benefit structure favours a more solitary lifestyle. Despite their potential to contribute heavily to fitness (Brent et al. 2013), the potential for temporal shifts in sociality received less focus. Among the most influential transitions is reproduction. For example, sexual selection drives some species of birds to gather on leks during reproduction (Bird et al. 2013).

Due to previous analytical limitations related to dependent data structure, repeatability, and community detection (Croft et al. 2011, Yang et al. 2016), the investigation of temporal based hypotheses have not received the same attention as other aspects of SNA. However, with the advancement of this relatively new field, there are new developments in SNA to fill these gaps. Specifically, exponential random graph models (ERGMs) have become increasingly common in SNA, as they deal with the dependent nature of network data. That is to say, when individuals in

a network are interacting, they are inherently dependent on whether another individual is available for a pair-wise interaction. In order to address this violation of the assumption to require independent data for analysis, ERGMs compare the observed data structure with potential alternatives. These ERGMs have allowed for hypothesis testing of homophily (i.e. the tendency of individuals to interact based on phenotypic matching) in a network, reciprocity, and social influence (Silk and Fisher 2017). However, to date, *temporal* ERGMs have not been used in ecological studies, but they offer the ability to detect stability within a network over time and explore temporally-driven hypotheses (Silk and Fisher 2017).

Black-tailed prairie dogs (*Cynomys ludovicianus*, hereafter 'prairie dogs') are a small (<2 kg), semi-fossorial, herbivorous rodent. They live in large social colonies, split into breeding units called coteries (Hoogland 1995). Previous work has revealed that coteries contain one breeding male, several breeding females, and associated yearlings and juveniles (Hoogland 1995). Males typically disperse as yearlings to form their own coterie with unrelated females (Hoogland 1995). Individuals within a coterie often exhibit affiliative social behaviours including allogrooming and communal nursing, which may aid in improved survival and reproductive success (Hoogland 1995). However, there is also documented evidence of agonistic social behaviours such as infanticide by nearby females in an effort to increase the chances of their offspring's own survival (Hoogland 1995). This juxtaposition of behaviours becomes particularly interesting because the same females that attempt to kill another female's offspring in the period prior to the emergence of juveniles from the natal burrow (i.e. the pre-emergence period) are those that will nurse those young if her own offspring do not survive to the emergence period (Hoogland 1995). The ability to cooperate (using affiliative behaviours) or defend offspring (using agonistic behaviours) likely plays into individual success of such a social animal. Hoogland (1995) has determined that females are highly aggressive after parturition to best increase their own litter's chance of survival (Hoogland 1995), but the level of aggressive behaviour has not been quantitatively analyzed in terms of reproductive output.

2.1.1 Objectives

The purpose of this study was to describe the social network of a prairie dog colony through behavioural observations and examine the variation in social structure with a multi-level approach: between communities, between individuals, and within individuals, as well as test hypothesized correlates of the social structure. Specifically, I tested the following hypothesized

correlates, previously found to be influential in other species: age (Hassett et al. 2010), sex (Ruckstuhl 2007), body size (Archie et al. 2006), kinship (Viblanc et al. 2016), spatial arrangement (Leu et al. 2011), and temporal arrangement (Oh and Badyaev 2010). Social networks for the pre- and post-emergence periods were constructed to observe changes in sociality over the course of reproduction. I tested inter-related hypotheses to explain temporal variation in sociality as a means to best exploit the trade-offs of sociality:

a. Individuals will differ in who they socialize with
b. Individuals will differ in how much they socialize
c. Individuals can vary these aspects of sociality over time

As the breeding season is also the period of largest dispersal of yearlings (Hoogland 1995), social bonds are the most dynamic as well. During April and May, individuals are continuing to identify familiar and unfamiliar individuals, while defending from invading yearlings, resulting in potentially more social interactions overall during this period. At this time, females may also have lower sociality as maintenance of their litter is of highest priority.

Body condition, measured as an index of body mass against skeletal size, may be an indicator of stable social relationships in prairie dogs through the ability to successfully defend resources through cooperation with coterie members and agonistic interactions with unfamiliar conspecifics. The Canadian population of black-tailed prairie dogs is unique in that it is the only population known to regularly hibernate (Gummer 2005, Lehmer 2006). As a consequence, body condition is potentially more closely tied to overwinter survival as annual changes in body mass where body reserves are added in the autumn to sustain a prolonged period of hibernation with no/limited access to food resources (Buck and Barnes 1999). These on-body energy reserves, primarily fat and protein, are obtained during the post-emergence season by actively defending desirable resources in their territories (Buck and Barnes 1999). Both male and female adult prairie dogs will actively defend the coterie territory and preferential resources, while gaining mass in the post-emergence period of the year (Hoogland 1995). Successfully defending resources through cooperation should increase the foraging success of members of a coterie and consequently, is reflected in their body condition. The prairie dog system offers a unique environment for temporal ERGMs to explore the stability of social networks over time, given their dynamic body condition over the year.

Furthermore, as evaluating temporal variation in a social species has been primarily understudied, the dynamic changes in prairie dog life history offers an ideal opportunity to study with aspect of SNA. Specifically, I addressed the fine-scale behavioural variation across the reproductive period and analyzed this from the individual level and the network level as a multi-level approach.

2.2 Methods

2.2.1 Study area

All data were collected from a single colony located in Grasslands National Park (49° 3' N, 107° 21'W) during July 2016, April 2017, and June 2017 (hereafter as 'pre-emergence' for April and 'post-emergence for June and July). Emergence refers to juvenile emergence in May. The colony, located in the Frenchman River Valley, occurs in the mixed grass prairie ecoregion of Saskatchewan (Wickens 1998), with a semi-arid climate (McGinn 2010). The area is dominated with short grass prairie species of which blue grama grass (*Bouteloua gracilis*) dominates, as well as cacti, forbs, and shrubs (Wickens 1998). The colony occupies an area of approximately 100 ha, with a road bisecting two portions. There are an estimated 800 adult prairie dogs on the colony (unpublished data). In order to document the social network in detail, I focused on one subsection of the colony. The area of the colony where I focused my study was chosen based on the complete census of this area as part of an ongoing study, where all individuals were individually identifiable, and the area contained a mix of adults and yearlings of both sexes. This area also contained individuals that were habituated to human presence such that observers were presumed not to affect their natural behaviour. In order to properly describe social networks, each prairie dog in the network had to be identifiable for behavioural observations. As part of the ongoing study, individual prairie dogs have been captured and marked as juveniles, so I had detailed information of their age and natal coterie. Immigrating individuals received tags and marks throughout the trapping season to have accurate identification of all animals in the area.

2.2.2 Data collection

2.2.2.1 Individual identification and measurements

For immigrating animals, the trapping methods are described as follows: I captured prairie dogs with Tomahawk live traps, baited with a mixture of peanut butter and oats. The amount of bait is considered negligible to the prairie dog diet and should not impact the success of each prairie dog. Upon first capture of an individual, I tagged the prairie dog in each pinna with unique alphanumeric tags for identification while handling (National Band & Tag Company, Newport, Kentucky, US). Additionally, I painted each prairie dog with a unique symbol on the dorsal pelage using Nyanzol-D to permit individual observation from a distance. Nyanzol-D leaves a distinct black mark without damage to the hair or skin and does not impact behaviour (Hoogland 1995). This ensured correct identification of each prairie dog within the social network. On capture of each individual, I recorded their sex, age (yearling or adult), and reproductive status (breeding or non-breeding). I assessed reproductive status based on examination of genitalia for males and pregnancy status of females.

I also collected morphological data for assessing body condition. These morphological attributes are body mass, length of the right hind foot, and zygomatic arch breadth. I measure body mass with a spring scale to ± 10 g (Pesola, Switzerland). I took three right hind foot measurement with a modified ruler to 1 mm of accuracy by measuring from the heel of the foot to the end of the longest toe (not including the claw). I took three zygomatic arch measurements with a caliper (Mastercraft) to 1 mm accuracy by measuring across the prairie dog skull at the widest point of the zygomatic arch.

I used these three measurements to create a body condition index following previous studies of small mammals (Schulte-Hostedde et al. 2001), modified from Iskjaer et al. (1989) and Pimental (1979). I completed a principal components analysis using log-transformed values of zygomatic arch length and right hind foot length to create a value for skeletal body size (Iskjaer et al. 1989). I then regressed body mass on the first principal component (PC1) of the body size, Pimental 1979), and the residuals of this regression served as the index for body condition (Schulte-Hostedde et al. 2001). Animals with larger body mass for a given body size were considered in better body condition than animals of similar body size and smaller body mass.

I marked and measured 67 individuals, in 8 coteries, across both sampling years. I used the same area across all sampling periods in order to observe changes in the network between these periods.

2.2.2.2 Social behaviours

I constructed social networks using pair-wise behavioural interactions. I observed these behaviours through binoculars (8-24x25mm, Nikon Aculon) as I sat on the ground at a distance of > 40 m from the individuals to limit human disturbance. I recorded the behaviours using all occurrence sampling observation techniques (Lehner 1992). Prairie dog social interactions occur at a rate low enough that all social interactions could be recorded for a set number of animals concurrently. Activity cycles for ground-dwelling sciurids vary over the year due to photoperiod length and reproduction (Everts et al. 2004) and the timing of observations was adjusted to reflect the change in activity peaks. This followed the method of SNA research for other species of ground-dwelling sciurids (Verdolin et al. 2014, Viblanc et al. 2016). I recorded the observations during the pre- and post-juvenile emergence time periods to compare how the social network may change during reproduction (Hoogland 1995).

I recorded both affiliative and agonistic interactions between pair-wise groupings. Affiliative interactions were categorized as encounters with only amicable behaviours including greet-kissing, allogrooming, jump yipping, and vigilance and foraging within a < 1 m distance (Hoogland 1981). Greet-kissing between prairie dogs is used to help identify each other by sniffing the face and locking teeth with each other, while allogrooming promotes affiliative relationships through removing potential parasites and reinforcing social bonds (Hoogland 1995). Jump yipping is a means to maintain social bonds and demonstrate an 'all clear' with surroundings animals by emitting a distinctive bark and thrusting the body vertically to increase visibility (Smith et al. 1976, Hare et al. 2014). It is thought to demonstrate the presence of the initiating animal and repeated by surrounding neighbours to establish who are nearby (Hoogland 1995). Animals that jump yip without a response from neighbouring animals are much more vigilant to predator presence and alarm calls from unrelated animals (personal observations) and is therefore a key behaviour in vigilance and communication.

Typically, agonistic encounters begin with affiliative behaviours, but then escalate to chasing or fighting (Hoogland 1995). Verdolin et al. (2014) reported a low rate of agonistic

interactions for Gunnison's prairie dogs (0.016 events/h among males and 0.013 events/h among both sexes). This is likely to also be the case for black-tailed prairie dogs as they live in similar social groups (Travis and Slobodchikoff 1993), however, the frequency of agonistic interactions likely varies over reproductive seasons due to potential for infanticide. Despite their rarity, agonistic interactions are highly indicative of a breakdown of the social cohesion typically found within a group. In this way, it was essential to observe the entire encounter to determine the type of interaction that has occurred.

I scored the encounters for intensity and frequency following standard protocols for animal behaviour studies (Martin and Bateson 2007). By scoring the behaviours, it provided a more detailed image of the social structure and highlights the range of relationships (Croft et al. 2008). I ranked the interactions according to their intensity, described in Table 2.1, where passive interactions received a low ranking and active interactions received a high ranking. For example, grooming is considered the most intense behaviour as it is an active interaction that benefits the receiver in contrast to proximal foraging, which is a passive interaction with little commitment to adjacent individuals (Hoogland 1995). I recorded frequency simply as the number of times two individuals interacted over the observation period.

2.2.2.3 Spatial and familial data

As social relationships of prairie dogs are likely to be influenced by their spatial arrangement, I also recorded the home range for each individual prairie dog within the social network in 2017 (Viblanc et al. 2016). I set up a flagged 15 x15 m Cartesian grid system to record locations of activities to establish the centroid and size of their home range. I recorded the UTM of the grid system and the burrow system for proper location of each individual. I recorded the location (< 1 m) of each individual's activities during a 20-minute focal scan randomly selected during activity peaks. I did two focal observations, separated by at least 3 days, for each prairie dog in both the pre- and post- juvenile emergence periods. For each set of focal observations, I overlaid the points to ensure the extent of the home range was captured after the second set and did require additional sampling. An average of 49 locations was recorded for each home range. By comparing the spatial and social networks, a comprehensive understanding of the relationship between home range and its impact on social behaviours can be established (Viblanc et al. 2010, Dobson et al. 2012). I found the centroid (central point of activity) of each

home range for each prairie dog using the kernelUD function in package adehabitatHR (Calenge 2006). Then I calculated the distance between all home range centroids, and created a matrix, where individuals with a low value are close together, and high values indicate individuals further away. For the 2016 period where I did not record home ranges, I used the most common trapping location as the centroid point of activity and created a matrix in the same method as for 2017.

In addition, social relationships are highly influenced by the presence of kin (Hoogland 1995). Individuals who disperse tend to remain near kin, especially females. This choice to remain near kin is likely influenced by social preference. In order to measure the dependence of social interactions on kin recognition and preference, I used known maternities from previous years' data to establish a matrilineal (as paternities were unknown) kinship matrix with the kinship2 package (Therneau and Sinnwell 2015). Individuals could score between 0 and 1 for relatedness, where a value of 0 was not related at all and a value of 1 represented sharing 100% of their genes (i.e. the level at which an individual is related to itself or monozygotic twin). For example, individuals from the same litter scored 0.50 as they share 50% of their genes. In some sciurid species, multiple paternities have been identified in a single litter (Hare et al. 2004), however, it is suggested that in prairie dogs, the coterie male sires an entire litter in 95% of all litters (Hoogland 1995).

2.2.3 Network construction

I placed the data collected from pair-wise interactions into a matrix using weighted scoring. Weighting is represented by a range of numbers where high values indicate intense encounters and low values represent passive encounters. I used the software Gephi (v. 0.9.1, Bastian et al. 2009) to create the social network structure from the inputted weighted matrix (Appendix B), where edges of the network display the weighting of the behaviours by using thicker lines for stronger connections (identified by intensity of behaviours). I did not include directed edges in my networks, as some of the behaviours I had observed are not directed, including proximal foraging, proximal vigilance, and jump yips, which made up a large part of the interactions in the network.

2.2.4 Data analysis

All analyses were completed in R (v. 3.4.1, R Core Team 2017), with most SNA occurring within the Statnet Project (Hunter et al. 2008). I created the social network data structures with the igraph (v 1.1.2, Csardi and Nepusz 2006), sna (Butts 2016) and network (Butts 2015; Butts 2008) packages. All analyses were based on these initial data structures. I calculated network metrics (network density, transitivity, and average degree) for each network, in order to compare network properties. Network density indicates the number of connections in the network and compares to the total number of connections possible, while transitivity measures how well information can travel across the network. Average degree is simply the average number of connections for each node. I used these metrics to determine if models for the networks should be run together or separate based on the differences in their network properties.

2.2.4.1 Community detection

As the prairie dogs have sub-communities within the colony known as coteries, I wanted to investigate if SNA could find this coterie structure. I used the community detection algorithm 'spinglass' (based on the Potts model; Wu 1982) as the sample size was <100 for each affiliative network (Yang et al. 2016) found in the igraph package (v 1.1.2, Csardi and Nepusz 2006). The community structures defined by the detection algorithm were compared to traditionally derived coterie membership. Traditionally, coteries were delineated by observing the shared space use of the individuals and the locations of agonistic encounters, indicating boundary lines of each coterie. The coterie membership between the traditionally defined coterie and the 'spinglass' coterie were compared with a chi-squared test. I did not analyze the agonistic networks for coterie structure, as the agonistic interactions indicate a break-down of the social structure and suggests individuals that are not positively affiliated as found in a coterie structure.

2.2.4.2 Arrangement in the network

In order to investigate the factors that predicted the social arrangement of prairie dogs, I used exponential random graph models (ERGMs). Social network data are inherently non-independent, and therefore, linear models alone are not a suitable metric for social network analysis. In ERGMs, the observed network is compared with possible alternative networks to determine if the relationships found in the observed network are non-random. The independent

terms in an ERGM can include dyadic covariates, node-based covariates, and structural covariates. I used the ergm (Hunter et al. 2008, Handcock et al. 2017) and ergm.count (Krivitsky 2016) packages as I had weighted edges in my matrices. I included relatedness and spatial arrangement as dyadic covariates, and age, sex, and body condition as node-based covariates. As I wanted to determine the degree of homophily in the network, the age and sex terms were set up as 'nodematch' functions. These functions allow the ERGM to determine the degree to which individual prairie dogs are interacting with others based on shared sex, age, home range or kinship. Each of the five networks was run separately in the model in order to compare differences between time periods and behaviour types.

2.2.4.3 Temporal stability in body condition

Body condition is a continuous variable and can change over time, therefore, I used a temporal ERGM to further explore this relationship. I expected that body condition would correlate with social rank because high rank should enable access to preferential resources through having affiliative social interactions on a larger portion of the landscape. In turn, good body condition may then enable them to maintain their social rank. Temporal ERGMs help to decipher this cyclical relationship. I used the package tergm (Krivitsky and Handcock 2015). In temporal ERGMs, there are two models: the formation model and dissolution model. The formation model predicts the likelihood for new edges to form between nodes, while the dissolution model predicts the likelihood for previous edges to dissolve between nodes. I ran two separate temporal ERGMs on affiliative networks. The first included only adults across all 3 time periods of study, while the second included all individuals from the pre-emergence period and following post-emergence period. This allowed me to include yearlings, that were not accounted for in the previous year. I did not complete temporal ERGMs for agonistic networks as the sample size for the post-emergence period was too small to validate.

2.2.4.4 Individual level predictors

For each individual in each network, I calculated four metrics of centrality using the igraph package (Csardi and Nepusz 2006). Degree centrality is simply the number of edges each node possesses and is therefore, a simple metric to calculate (Croft et al. 2008). Strength is the sum of the weighted interactions, as it considers the intensity of the behaviour. Betweenness

centrality (B_i) is calculated as the total number of shortest paths between pairs of nodes (other than i) that pass through i (Croft et al. 2008). Due to weighting of the edges in the network, I used modified methods to account for these weights as described by Opsahl et al. (2010). Betweenness centrality was useful in determining the key individuals within a network. Those with high betweenness scores are considered the 'hubs' of the network, connecting sub-sections together. Eigenvector centrality describes the secondary centrality of an individual. It examines how well connected an individuals' connections are. Those with high eigenvector centrality are within highly connected areas of a network.

I collapsed the four social network metrics using principal component analysis (PCA) in the vegan package (Oksanen et al. 2017) to better describe centrality within the networks. I used 2 major axes (principal components; PCs) to describe centrality, with between 83 – 100 % of the variance explained by these axes (see Appendix A). The first axis (PC1) describes the overall number and quality of connections in the network (high degree and high strength, as betweenness centrality and eigenvector centrality were orthogonal to PC1). The second axis (PC2) described the 'location' of an individual within the network, where a high PC2 value indicated an individual that connected coteries, while a low PC2 score indicated an individual that was well-connected within its own coterie. These two axes will be described as 'centrality' and 'connectedness' for PC1 and PC2, respectively. To describe these axes using Figure 1.1, a high centrality value would describe node 10 as this node has 6 edges, while nodes 4 and 9 would have low centrality values. For connectedness, node 3 would have the highest value as this node connects two sub-communities, while nodes 5 and 10 would have the lowest connectedness value as they are only connected within their own sub-community. It is important to note that individuals that are peripheral in the network do not necessarily exist on the periphery of the study area, as social connections separate from spatial area.

I ran general linear models for normally distributed network data. General model assumptions were checked for all models by plotting residuals, as well as Q-Q norm and leverage plots. The covariates I included in each model were reproductive status, body condition, coterie size, and home range size. Home range was only included as a covariate for the 2017 data, as 2016 home range centroids were established through trapping locations and did not encompass their full home range. I excluded age from these analyses as reproductive status is collinear given that most adults of at least two years are reproductive, while yearlings are

typically not. Reproductive status was also split for males and females as prairie dogs have a polygynous mating system (Hoogland 1995).

As described earlier, network data are not independent (Croft et al. 2011). In order to account for this non-independent nature, I randomized the network data with permutations in the igraph package (Csardi and Nepusz 2006). In addition, as the social network data are not independent of the spatial network, I kept the spatial location of each node static, while allowing the centrality metrics to vary (Viblanc et al. 2016). I permuted 1000 randomized social networks and ran linear models for normally distributed network metrics. This resulted in 1000 estimates for each variable. I compared the simulated estimates (and standard errors (SE)) with the original data using a Welch's t-test, as this accounts for both unequal variance and unequal sample size

All procedures followed the Canadian Council on Animal Care guidelines for wildlife and were approved by the University of Saskatchewan Animal Care Committee (AUP 20140042).

2.3 Results

Five social networks were constructed over three sampling periods from 264 hours of observation (Table 2.2). One affiliative network was built for each time period: July 2016 (n = 22), April 2017 (n = 57) and June 2017 (n = 36). Agonistic networks were built for April 2017 (n = 50) and June 2017 (n = 13). During July 2016, only one agonistic interaction was observed, therefore, eliminating the agonistic network in this sampling period. There was a decrease in the rate of social interactions for both agonistic and affiliative behaviours from the pre- to post-emergence season. On average, there were 0.36 agonistic interactions/individual/hour during the pre-emergence period, while 0.06 agonistic interactions/individual/hour during the post-emergence period. In contrast, there were 1.52 affiliative interactions/individual/hour during the pre-emergence period and 0.67± 0.10 SE affiliative interactions/individual/hour during for post-emergence period. The increased affiliative and agonistic interactions in the pre-emergence period also correspond with a higher adult and yearling density during this time period, and an increase in average degree centrality for each individual (Table 2.2).

Network density and transitivity were highest in 2016 and decreased in each following sampling period (Table 2.2). The 2016 post-emergence network, despite having the lowest

spatial density in all time periods, had the highest network density and transitivity, indicating that social interactions are driven by more than just overall density.

2.3.1 Community detection

Figure 2.1 depicts all social networks across all sampling periods. The 'spinglass' community algorithm was able to detect the coterie structure within each of the affiliative networks (Figure 2.1). There was no significant difference ($X^2 = 4.89$, df = 11, $p = 0.93$) between the coterie membership generated by the traditional method and the 'spinglass' method. However, there was one instance where the algorithm selected a coterie in the 2017 post-emergence network that did not exist (Figure 2.1, panel c). The two individuals in this separate structure belong to the coterie overlapping this structure in the figure. These two individuals interacted more with each other than others in the coterie, however, they occupied the same space as the other structure. The number of individuals in a coterie ranged from 2 to 14, with an average of 6.61 ± 1.06 SE.

2.3.2 Arrangement in the network

Tables of full and final ERGMs are provided in Appendix A. The predictors of the likelihood of a social tie to occur were variable between networks, but there were some common signals for affiliative networks. For all affiliative networks, distance and age were significant ($p < 0.05$) predictors. The closer together two individuals were in space, the more likely they were to form ties. As well, yearlings were more likely to associate with other yearlings, while adults tended to associate with other adults. In the 2016 post-emergence network, sex ($p = 0.002$) and body condition ($p < 0.001$) were also significant predictors of sociality, with individuals more likely to associate with their own sex and their same body condition. In the 2017 post-emergence network, relatedness ($p = 0.001$) was a significant predictor of sociality, where individuals of higher relatedness were more likely to interact.

For both agonistic networks, sex ($p < 0.01$) was a significant predictor, where males and females were more aggressive to members of their own sex. For the 2017 pre-emergence agonistic network, age ($p = 0.001$) and body condition ($p = 0.001$) were also significant predictors, where individuals were more aggressive within their own age class and similar body condition.

2.3.3 Temporal stability in body condition

When looking at individuals across all three affiliative networks, body condition ($p < 0.05$) was a significant predictor of the changes in the network (Table 2.3). Individuals of poorer body condition were more likely to lose old connections and form new ones. For individuals within the second and third networks, body condition ($p = 0.003$) was a significant predictor of losing social ties only (Table 2.4). Individuals with poorer body condition were more likely to lose social ties, but not to form new ones.

2.3.4 Individual predictors

Tables of full and final models for all linear regressions can be found in Appendix A.

Reproductive status

The 2016 post-emergence affiliative network models revealed that centrality did not differ significantly across reproductive groups (reproductive females were not significantly different than non-reproductive females ($p = 0.94$) and non-reproductive males ($p = 0.34$; Figure 2.2, panel a), but there was a significant difference in connectedness between reproductive individuals and non-reproductive individuals. Reproductive females were significantly more likely to connect coteries than non-reproductive males ($p = 0.03$) or females ($p = 0.04$; Figure 2.2, panel b). In 2016, there was only one breeding male, and was therefore removed from analysis, but was included in Figure 2.2 for comparison.

The 2017 pre-emergence affiliative network models revealed that reproductive females were significantly less central than reproductive males ($p = 0.01$), and non-reproductive males ($p < 0.001$) and females ($p < 0.001$) (Figure 2.2, panel c). Additionally, reproductive females were less connected to other coteries than reproductive males ($p = 0.01$; Figure 2.2, panel d). Non-reproductive females ($p = 0.89$) and males ($p = 0.24$) had similar connectedness values as reproductive females, suggesting that reproductive males are connecting coteries in the pre-emergence period.

For the 2017 post-emergence affiliative network models, reproductive status was not a significant predictor for centrality or connectedness (Figure 2.2 panels e and f). Reproductive females did not differ significantly from non-reproductive females (centrality: $p = 0.30$, connectedness: 0.63), non-reproductive males (centrality: $p = 0.35$, connectedness: 0.48) or reproductive males (centrality: $p = 0.78$, connectedness: 0.66).

For the 2017 pre-emergence agonistic network models, reproductive females had significantly lower centrality values than reproductive males ($p < 0.001$) but were not significantly different from non-reproductive females ($p = 0.09$) or males ($p = 0.99$), suggesting that reproductive males are the most agonistic during this time period (Figure 2.3, panel a). Reproductive groups did not differ in connectedness (Figure 2.3, panel b). Reproductive females were similar to non-reproductive females ($p = 0.69$), non-reproductive males ($p = 0.81$), and reproductive males ($p = 0.34$) for connectedness.

The 2017 post-emergence agonistic centrality and connectedness were not predicted by reproductive group (Figure 2.3, panels c and d). Reproductive females did not differ from non-reproductive females (centrality: $p = 0.37$, connectedness: 0.53), non-reproductive males (centrality: $p = 0.27$, connectedness: $p = 0.26$), or reproductive males (centrality: $p = 0.11$, connectedness: $p = 0.31$).

Body condition

Body condition was not a consistent predictor across sample periods. For 2016, body condition was not significantly correlated with centrality ($p = 0.42$) or connectedness ($p = 0.32$). For the pre-emergence networks, body condition was positively correlated with affiliative centrality ($p = 0.02$), but not connectedness ($p = 0.79$). Individuals of better body condition had more connections than those in poor body condition, but these connections are equally likely to be with individuals of their home coterie or with other coteries. For the 2017 pre-emergence agonistic network, body condition was not a significant predictor of centrality ($p = 0.30$), but it was for connectedness ($p = 0.01$). Individuals of better body condition were more likely to be aggressive with individuals outside of their own home coterie. For the post-emergence networks, affiliative centrality ($p = 0.67$), affiliative connectedness ($p = 0.74$), and agonistic centrality ($p = 0.17$) were not correlated with body condition, but agonistic connectedness ($p = 0.01$) was significantly correlated with body condition.

Coterie size

Coterie size was not a significant predictor for sociality in most networks. For the 2016 post-emergence network, centrality ($p = 0.11$) and connectedness ($p = 0.15$) were not correlated with coterie size. For the 2017 pre-emergence networks, coterie size was not a significant predictor of affiliative centrality ($p = 0.99$), but affiliative connectedness was positively correlated ($p = 0.01$). Coterie size did not predict centrality ($p = 0.27$) or connectedness ($p =$

0.48) in the agonistic network. For the 2017 post-emergence networks, a similar pattern was found as for the pre-emergence networks. Coterie size did not significantly predict affiliative centrality ($p = 0.66$), but it was positively correlated with affiliative connectedness ($p = 0.04$). Again, coterie size did not significantly predict centrality ($p = 0.53$) or connectedness ($p = 0.10$) for the agonistic network. Therefore, coterie size was only predictive of affiliative connectedness for 2017 networks.

Home range size

Home range was not a consistent predictor for sociality across the sample periods. For the pre-emergence networks, home range was not a significant predictor for affiliative centrality ($p = 0.23$), but affiliative connectedness was positively correlated with home range ($p = 0.01$). This suggests that individuals with larger home ranges are more likely to interact more with individuals outside their home coterie; however, this was only true for the affiliative interactions, as there was no correlation between home range size and agonistic principal components (centrality: $p = 0.67$, connectedness: $p = 0.99$). For the post-emergence networks, home range was not a significant predictor for affiliative centrality ($p = 0.08$) or connectedness ($p = 0.78$) but showed a positive relationship for agonistic centrality ($p = 0.03$) and connectedness ($p = 0.01$). Again, this suggests that individuals with larger home ranges in the post-emergence period are more likely to encounter unfamiliar individuals outside of their own coterie, increasing the likelihood of agonistic interactions (Figure 2.4).

2.4 Discussion

I sought to explore variation of sociality between and within individual black-tailed prairie dogs at multiple levels of social organization. Other studies have examined this multi-level approach at static time points (Sosa 2016, Verdolin 2014), while others have looked at the temporal impact of social variation (Silk et al. 2017, Oh and Badyaev 2010), but my study has attempted to bridge these two components. In addition, I tested a number of correlates at each level (coterie: kinship, spatial arrangement, age, sex, and body condition; between individuals: reproductive status, home range, coterie size, and body condition; within individuals: season and body condition). My results suggest that there is both between and within individual variation of sociality as both rates of social behaviour and social roles changed across the reproductive season. Overall, there was variation between individuals within a sampling period, as well as

variation in the same individuals across sampling periods. The most significant and reliable predictor of variation was reproductive status. Females reduced their affiliative sociality to focus on foraging and lactation in the pre-emergence period. It appears that life history timelines are impactful to rates of social interactions as the pre-emergence period saw more interactions of both affiliative and agonistic nature as well as having more consistent predictors compared to the post-emergence period. Additionally, social roles in prairie dogs appear to change across seasons, where reproductive females maintain social connectedness between coteries in the post-emergence period, while reproductive males assume this role in the pre-emergence period. This change in individuals occupying central roles suggests a plasticity in prairie dog sociality and maintenance of roles.

2.4.1 Community variation

Social network analysis found coterie sub-structure within a network using community detection algorithms, that corresponded with coterie identification using traditional methods. However, these coteries did not resemble the coterie structure in other (more southern) populations, described by Hoogland (1995). Approximately 50% of the coteries (10/19) in my sutdy had a breeding male across all time periods. However, the coteries without breeding males defended their territory in the same manner as coteries with reproductive males, where males spend more time defending the territory than females. The coteries without breeding males were typically made up of yearlings of both sexes and were typically much larger than others (upwards of 10 individuals). In two instances, this was due to fusion of litters with dams that had died or disappeared in previous months.

This difference in coterie make-up may be due to environmental differences across the geographic range. As my study occurred at the northern extent of the range, there may be additional pressures altering the social structure. Smith et al. (1973) found that prairie dogs typically establish home range boundaries and coteries during the winter, which relax in the summer period. As my study population occurs at the northern periphery of the range where they experience harsher winters, inducing hibernation, the timing of setting up coterie boundaries and coterie membership may be constrained to the spring, leading to alternative coterie structures. However, in the two years that this study occurred, the population was growing due to an abundance of resources and relatively milder weather (Environment Canada 2017). Potentially,

this increase in resource abundance may promote larger or atypical coteries. For example, a study on the social structure of great gerbils (*Rhombomys opimus*) suggested that the actual grouping arrangement was based on ecological constraints of the habitat (Randall et al. 2005). In years with an abundance of resources, individuals would often form philopatric colonies, however, if resource abundance was poor, individuals would separate into individual units (Randall et al. 2005). This plasticity of sociality due to resource abundance may be similar to the prairie dog social system.

There was variation between communities in terms of the types of individuals that made up each coterie. Some coteries were dominated by yearlings, who had higher rates of social interactions and as a result, sociality varied between communities. In terms of affiliative networks, individuals tended to associate with others located nearby in space and of the same age, while sex and relatedness were important for 2016 and 2017 post-emergence, respectively. There is a clear relationship between space use and social interactions, as individuals are relatively loyal to their home range, getting 99% of their resources from this area (Hoogland 1995). Individuals are thus much more likely to interact with individuals that share their home range. The groupings of adults together and yearlings together suggests a breakdown of typical social relationships. There is also evidence that populations segregate based on age due to differing activity levels and behavioural incompatibility. Yearlings have different priorities than the reproductive adults, especially for yearling males that are dispersing to a new coterie. Similarly, in macaques, yearling males are known to self-segregate from all other groups which is indicative of differing behaviour types (e.g., play-fighting) from other sex/age groups of macaques (Hasset et al. 2010). There is additional evidence for behavioural incompatibility in polygamous ungulates, suggesting divisions based not only on age or sex, but for social phenotypic matching (Bon and Campan 1996). Prairie dogs, as well, may be choosing to associate with similar behavioural intensities within a coterie as yearlings display higher rates of social behaviours.

For the agonistic networks, aggressive interactions occurring between the same sex are reflective of the biology of this species. During the pre-emergence period, males were more likely to be defending their territory from other males, while females were more likely defending against infanticide by other females. This is highlighted by age being a factor for aggression in the pre-emergence period, as typically adult females are reproductive, while yearlings are not.

The same phenomenon was described by Smith et al. (1973) where they found that black-tailed prairie dogs were consistently aggressive toward members of their own sex, but not toward members of the opposite sex.

2.4.2 Between individual variation

The results of the PCA on individual metrics of centrality revealed that individuals can take up different 'locations' within a network, either highly connected within a coterie or connecting multiple coteries together. This location within a network was represented by PC2, as often node betweenness centrality and eigenvector centrality were opposite directions in the PCA, while orthogonal to degree and strength. This highlights a trade-off between being connected to familiar individuals, but receiving less information overall, versus being connected to less familiar individuals but receiving more information overall.

Reproductive status was the most consistent predictor of variation in sociality. In both post-emergence social networks, reproductive role did not influence the overall sociality of an individual, but the pre-emergence network showed that reproductive females tended to have lower sociality than all other reproductive groups. Hoogland (1995) had suggested that reproductive females became highly aggressive in the pre-emergence period and became more affiliative in the post-emergence period. The reproductive females in my study were not more aggressive than any other group, and in fact, breeding males had the most aggressive interactions. This may suggest that breeding females are only interacting (both affiliative and agonistic) when necessary as their primary goals are caloric intake for lactation and defence of offspring from infanticide. Additionally, this demonstrates that sedentary species are able to manipulate their sociality as other motile or migratory species are able to but is less detectable as the spatial arrangement remains the same. This is an important consideration when assessing sociality based on proximity collars or photos as it does not capture the perceptive change in social interaction rates.

By incorporating a range of behaviours, I was able to capture true affiliative and agonistic behaviours. This in-depth behaviour gave further insights into how individuals not only choose who they are interacting with, but what type of behaviour they are exhibiting, which may delineate more about the energetic costs of sociality, and how individuals manage their energy budget in terms of maintaining social stability, but also appropriate defenses. Recently, many

advances have been made in using GPS-based contact/proximity collars in network analyses, particularly when looking at seasonal variation (Hamede et al. 2009, Theimer et al. 2016, Silk et al. 2017). When looking at contact collars or spatial proximity, the type of behaviour being exhibited is lost and weighted edges are interpreted as only the number of contacts made, without any context to the type or intention of the behaviour (Chen and Lanzas 2016). While studies typically acknowledge the gap in information gained through these collars, the extent of the information lost is not quantified. If my data were collected with only contact collars, the agonistic relationships would have been interpreted as affiliative, due to lack of context. I could not assume intention or intensity with these methodologies. Contact collars have been proven to be effective in studying disease transmission between conspecifics (Hamede et al. 2009, Silk et al. 2017), but other hypotheses in SNA may require actual behavioural analysis. Furthermore, Chen and Lanzas (2016) suggest that despite contact networks and social networks being similar in their capacity of analysis, there must be a distinction in terms of biological relevance and interpretation. My study suggests that contact or proximity alone are not sufficient for true social network analysis.

2.4.3 Within individual variation

Within individual variation of sociality was expressed in the transfer of social roles at different points of time. In 2016 post-emergence, the breeding females maintained the connectivity between coteries, while breeding males maintained the role during 2017 pre-emergence period when females were prioritizing foraging and lactation. There appears to be some plasticity of social roles throughout pre- and post-emergence periods of the year. Verdolin et al. (2014) reported that female Gunnison's prairie dogs (*Cynomys gunnisoni*) maintained the role of connecting different social groups as males are more likely to disperse from the population. However, betweenness centrality was not significantly correlated with age or sex. Their observations occurred from March to August, which encompasses the pre- and post-juvenile emergence periods of prairie dogs. By combining observations across the year, the individuals occupying "bridge" roles may be dismissed as the exchange of these roles occurs at a finer temporal scale.

Between time periods, I also found that reproductive females had reduced sociality in the pre-emergence period compared to the post-emergence period. In the post-emergence period, as

rates of social interaction were lower, it may suggest a dear enemy phenomenon is occurring (Fisher 1954), where the territorial boundaries between neighbours have been previously well-established in the pre-emergence period leading to reduced interaction in the post-emergence period. This phenomenon validates the importance of considering season for individual survival and fitness, especially during important periods of the year like lactation or dispersal. Additionally, this change in sociality over time underlines the importance of choosing the temporal range of when observations are taken as key behaviours may change over the season as in this study. Given these temporal changes, there may be a short window for in-depth observation to occur, and understandably, becomes more intensive when looking to capture fine-scale changes in sociality. While females reduced their sociality in the pre-emergence period, they did not alter they spatial range, calling to question the validity of using spatial proximity or home range overlap as a proxy for sociality, as I have shown that a population that maintains spatial structure can also manipulate their sociality. Therefore, understanding the specific life history and ecological traits of a species and the potential for variation in sociality are highly important for SNA.

2.4.4 Temporal stability in body condition

Individuals of poorer body condition were more likely to have social ties dissolve. This relationship suggests that better body condition helps to maintain the stability of an individual's social status within a group, while poorer body condition suggests that an individual is more likely to change coteries and increases their chance of dispersal. When yearlings were included in the temporal model, these individuals likely dispersed as they did not form new ties at a higher rate than individuals in better body condition. This study is the first instance of using temporal ERGMs with animal systems. This study has demonstrated how a phenotypic trait can create stability or instability within a network and that these traits are impactful to peak life history events.

2.4.5 Limitations

There are several components of my study that could be improved for future studies. As my relatedness data was limited to the matrilineal line, the relationship between coterie structure and relatedness may change if the patrilineal lines can also be identified and provides a new study objective for the future. Furthermore, while the individual level metrics of our study were

repeatable between the two post-emergence periods, the network level metrics were not. This may be due to a sample size issue in the first post-emergence period, or due to changing densities between years. A long-term study of the social dynamics of this population would clarify the patterns observed over two years of study and establish repeatability of variation across all three levels.

2.4.6 Overall conclusions

I have provided evidence for social variation at three scales within a group of black-tailed prairie dogs: community level, between individuals, and within individuals. This multi-level variation suggests that not only are species balancing the costs and benefits of sociality by modifying group size and density, but individuals are also balancing these trade-offs of group membership. I was able to examine in-depth social behaviour types over seasonal scales, which are often ignored by using passive recording (e.g., contact collars). My results suggest this passive recording may not necessarily capture the entire story, and it is important to discern the difference between contact networks and social networks. Furthermore, I was able to increase the understanding of the relationship between spatial arrangement and social relationships, where there is an inherent connection between them, but there are also fine-scale modifications in the social structure that may not be reflected in the spatial structure.

This study was the first to explore temporal ERGMs in a free-ranging wildlife population. I was able to quantify stability of sociality based on body condition. These data allowed me to empirically evaluate the extensions of new analysis tools for SNA for a wildlife population, especially in terms of temporal dynamics within a network. I was able to investigate the impact a physiological trait (body condition) had on social stability and maintenance, which may be unique to adults and not yearlings. Currently, however, analyses with temporal ERGMs are limited to continuous variables at this time, with the potential for categorical data to be analyzed in the future. This new analysis could further hypotheses of keystone individuals within a system or the presence/absence of particular traits creating stable social structures over long periods of time as some social systems are maintained across generations. Despite this limitation of restricting analysis to continuous variables, my study can be used as a basis to understand the specific costs and benefits an individual must balance when altering their sociality.

2.5 Tables

Table 2.1 The ranking system for weighting edges in a social network based on the affiliative and agonistic behaviours being displayed in pair-wise interactions.

Affiliative Behaviour	Agonistic Behaviour	Score
Proximal foraging (< 1 m apart) Mutual vigilance (< 1 m apart)	Tail raise Barking	1
Jump yipping Greet-kissing Anal sniffing	Chasing	2
Allogrooming	Fighting	3

Table 2.2 Summary statistics for five social networks of black-tailed prairie dogs across 2016 post-emergence, 2017 pre- and post-emergence. The sample size (nodes) and density of the sample area describe the population, while network density, transitivity, and average degree (± standard error) describe the overall connectedness of each network.

	Density (#/ha)	Nodes	Network Density	Transitivity	Average Degree
2016 post-emergence affiliative	44.0	22	0.216	0.600	4.545 ± 0.500
2017 pre-emergence affiliative	54.3	57	0.105	0.568	5.895 ± 0.370
2017 post-emergence affiliative	47.6	36	0.087	0.382	3.056 ± 0.287
2017 pre-emergence agonistic	54.3	50	0.057	0.223	2.800 ± 0.270
2017 post-emergence agonistic	47.6	13	0.115	0.000	1.385 ± 0.213

Table 2.3 Model estimates (± standard error) and significance for the formation and dissolution temporal random graph models for black-tailed prairie dogs (n = 22) from 2016 post-emergence to 2017 post-emergence. Bolded metrics indicate significance of $p < 0.05$.

	Formation Model			**Dissolution Model**		
Metrics	**Estimate**	**Std. Error**	**p-value**	**Estimate**	**Std. Error**	**p-value**
Edges	-4.387	0.307	<0.001	-0.072	0.242	0.765
Body Condition	**-0.004**	**0.002**	**0.044**	**-0.006**	**0.002**	**0.021**

Table 2.4 Model estimates (± standard error) and significance for the formation and dissolution temporal random graph models for individual black-tailed prairie dogs (n = 57) from 2017 pre- to post-emergence periods. Bolded metrics indicate significance of $p < 0.05$.

	Formation Model			**Dissolution Model**		
Metrics	**Estimate**	**Std. Error**	**p-value**	**Estimate**	**Std. Error**	**p-value**
Edges	-4.271	0.215	<0.001	-4.134	0.214	<0.001
Body Condition	0.000	0.002	0.906	**-0.003**	**0.001**	**0.003**

2.6 Figures

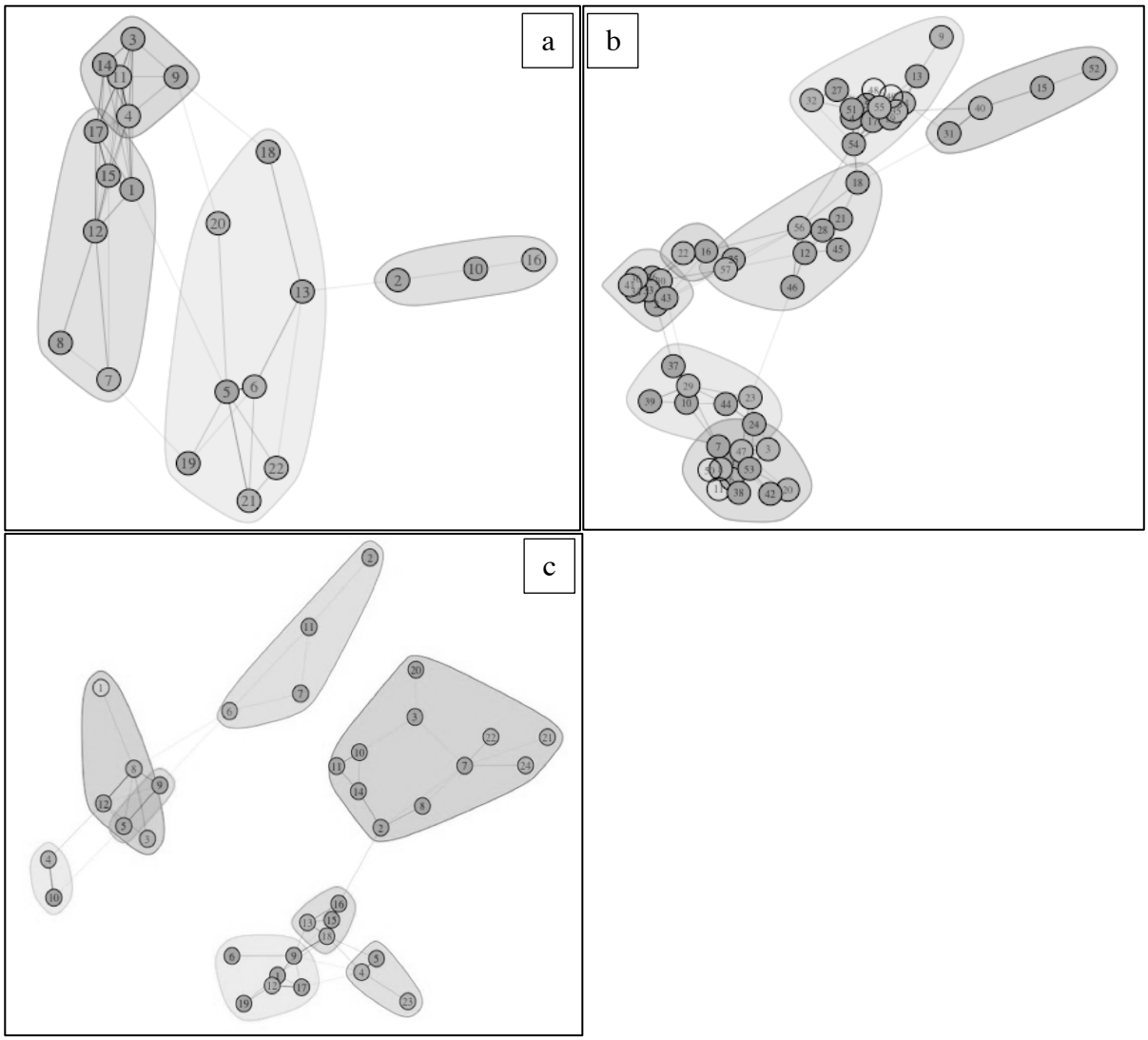

Figure 2.1 Affiliative social networks for black-tailed prairie dogs across all three sampling periods with the coterie structure predicted by the community detection algorithm shaded in grey. Panel a is 2016 post-emergence (n = 22), Panel b is 2017 pre-emergence (n = 57), Panel c is 2017 post-emergence (n = 36).

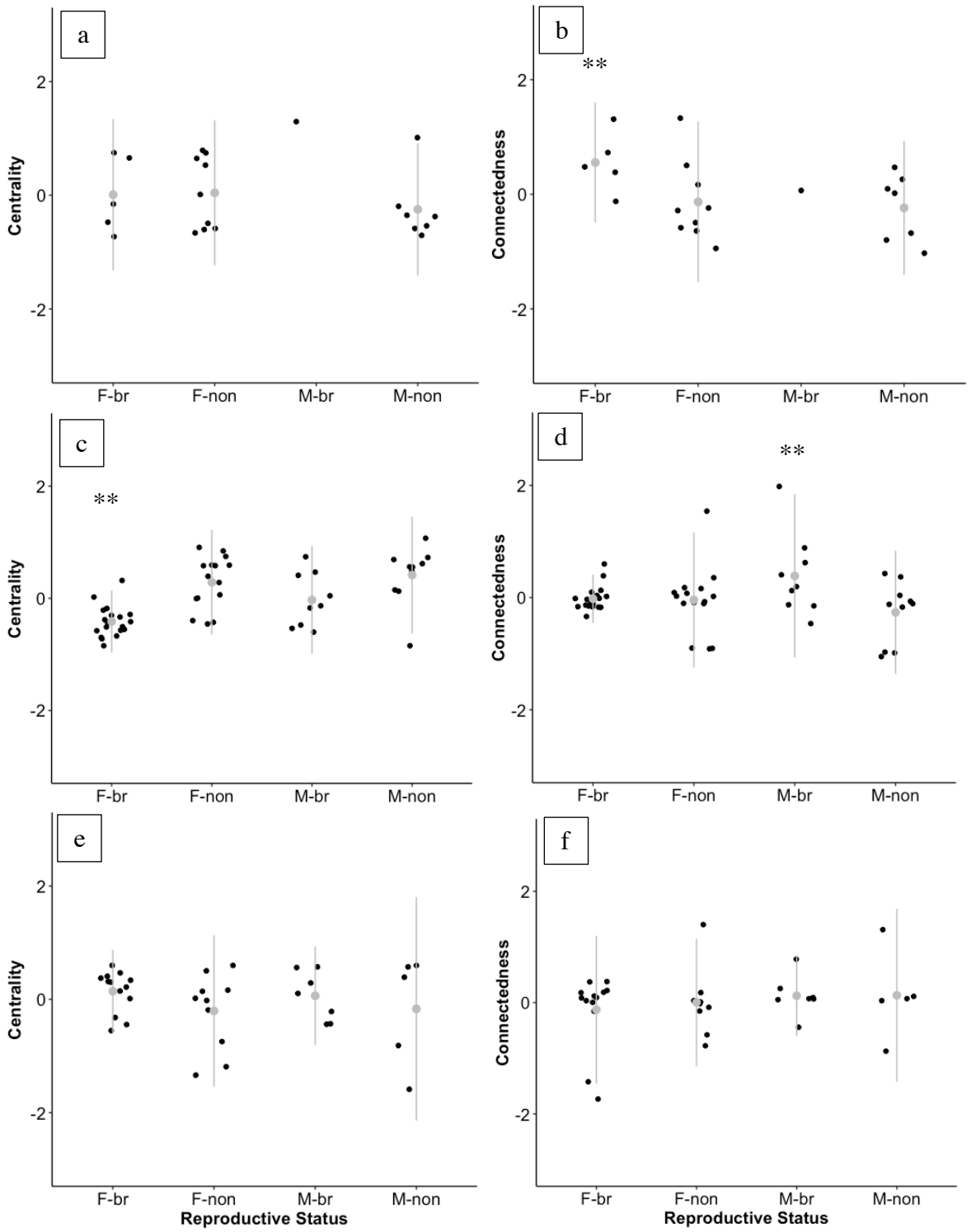

Figure 2.2 Jitter plots for centrality and connectedness for all affiliative networks in four reproductive status groups in black-tailed prairie dogs. The grey circle represents the mean and the grey bar is the standard deviation. Panels a and b are 2016 post-emergence (n = 22), panels c and d are 2017 pre-emergence (n = 57), panels e and f are 2017 post-emergence (n = 36). Significant differences are indicated with **.

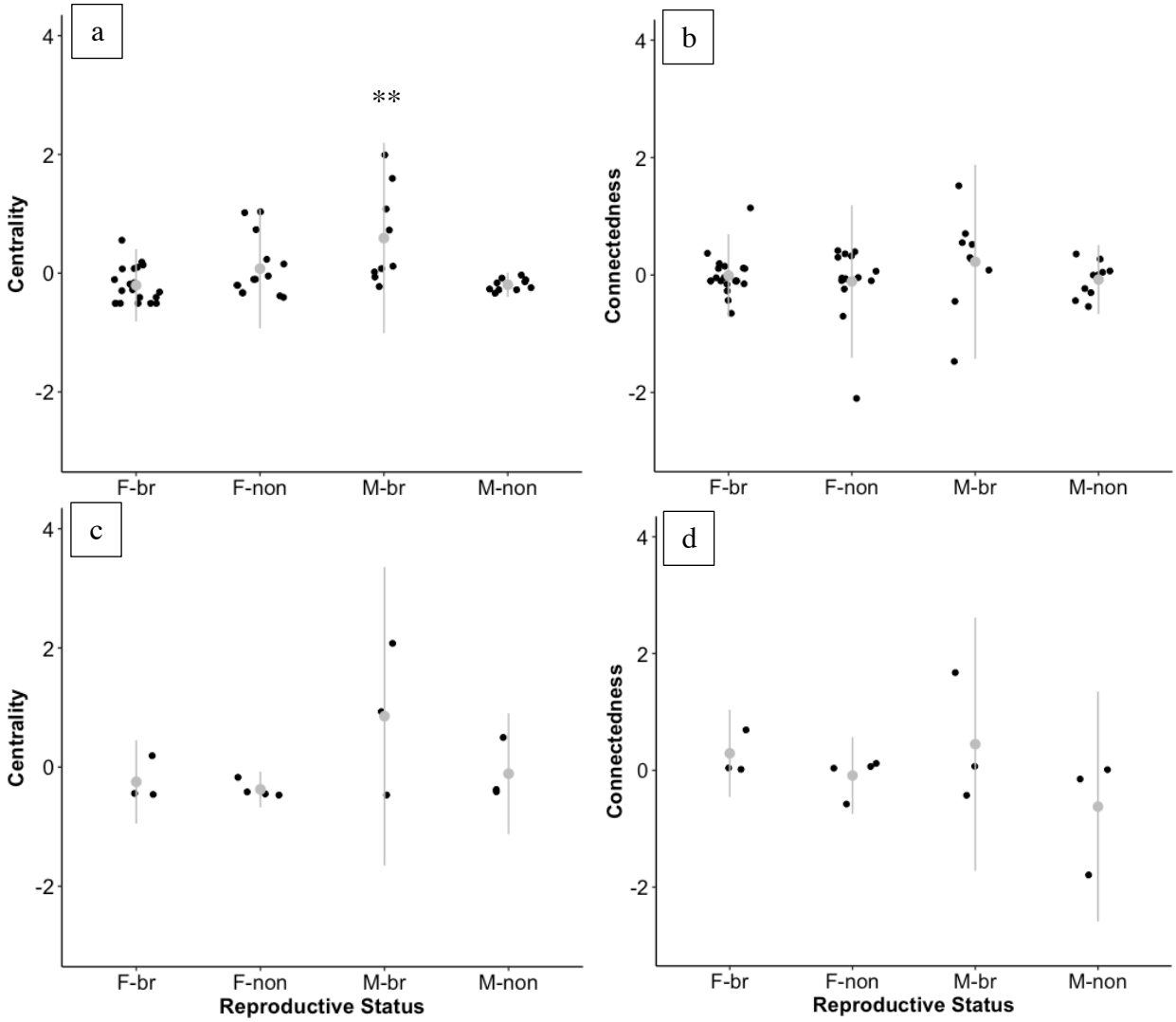

Figure 2.3 Jitter plots of sociality metrics (centrality and connectedness) for all agonistic networks across four reproductive status groups in black-tailed prairie dogs. The grey circle represents the mean and the grey line represents standard deviation. Panels a and b are 2017 pre-emergence (n = 57) and Panels c and d are 2017 post-emergence (n = 36). Significant differences are indicated with **.

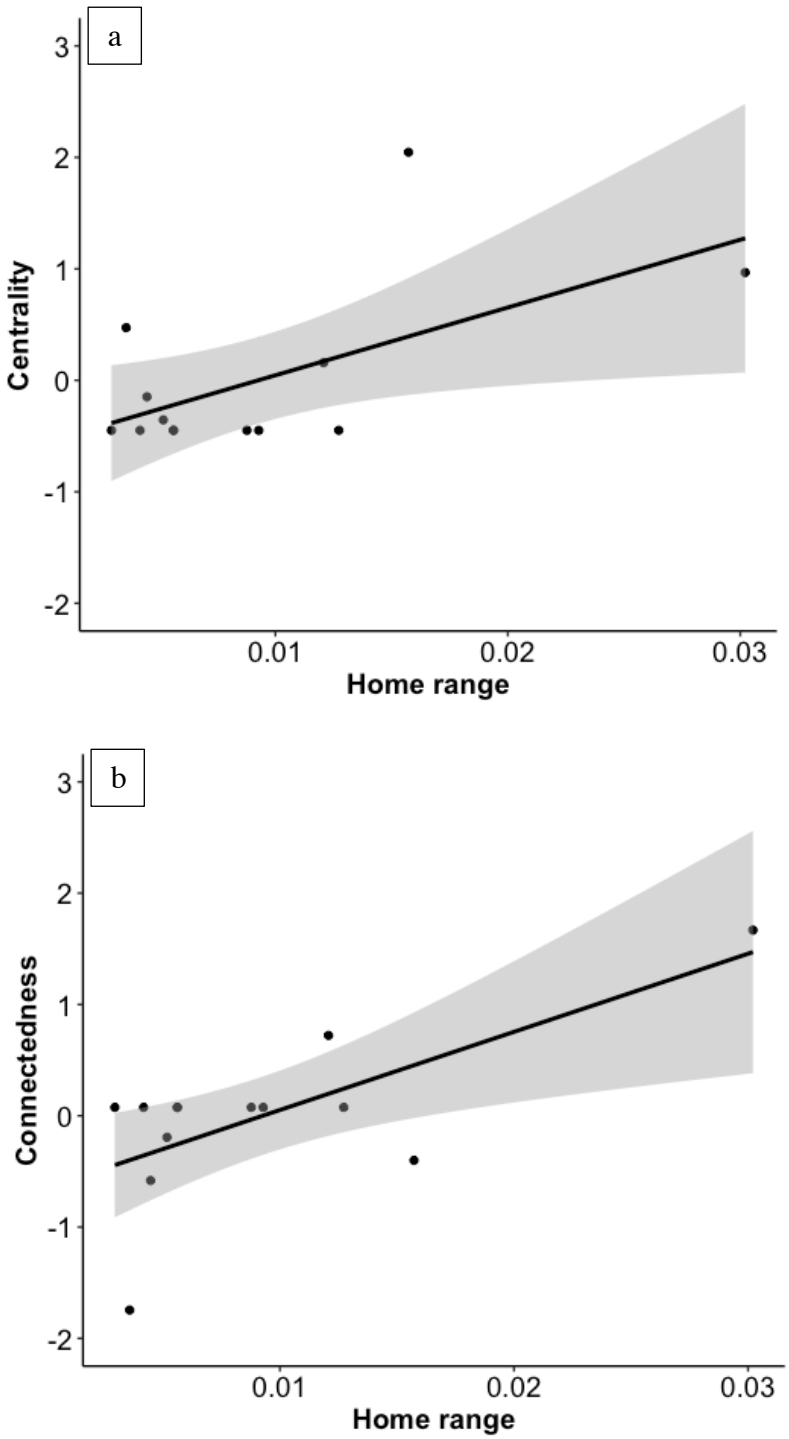

Figure 2.4 The effect of home range size (ha^2) on metrics of sociality (a) centrality and (b) connectedness for the 2017 post-emergence agonistic network in black-tailed prairie dogs (n = 13). Grey area represents the 95% confidence interval around the fitted line.

CHAPTER 3:

FITNESS CONSEQUENCES OF INDIVIDUAL VARIATION IN LEVELS OF SOCIALITY IN BLACK-TAILED PRAIRIE DOGS (*CYNOMYS LUDOVICIANUS*)

3.1 Introduction

Socio-biological theory suggests that variation in group living is the result of balancing costs and benefits that vary across taxa and environment (Krause and Ruxton 2002). In order for sociality to evolve, benefits (e.g., increased information exchange) must outweigh costs (e.g., resource competition). These costs and benefits are weighed at the individual level, where the decision to exist in a group must optimize fitness. Typically, the costs and benefits of group living are considered roughly equivalent across all individuals within the group and across all time periods, and that variation in these trade-offs results simply from density dependence (Krause and Ruxton 2002). For example, as population density increases, large social groups would be expected to experience lower reproductive rates and/or increased dispersal as the population nears carrying capacity and the costs related to intraspecific competition increase. However, treating levels of sociality as consistent across individuals and temporally invariant ignores the central premise of natural selection: individual phenotypic (including behavioural) differences influence individual fitness (Table 3.1; Croft et al. 2008, Blumstein et al. 2018).

Social network analysis (SNA) investigates how the variation in behaviours among individuals affects the social structure observed in the population (as explored in Chapter 2) as well as individual fitness. Fitness is defined here as the ability to successfully reproduce and contribute to the gene pool of the next generation (Maynard-Smith 1989). Social network analysis attempts to quantify the social behaviours of an individual through defining their centrality (the number of social connections, often expressed as degree in a network) or position (inter-connectedness of their various connections, described as betweenness centrality and eigenvector centrality) within a network. The centrality and position maintained by an individual in a network is assumed to be due to the attempt to optimize their fitness (Pizzari and Gardner 2012).

Increased reproductive success is a common benefit to centrality in a social network (Table 3.1). Oh and Badyaev (2010) found that male house finches (*Carpodacus mexicanus*) were able to increase their own attractiveness and chance of copulations by manipulating the number and types of network connections they had, by matching their social groups with their relative plumage attractiveness. For male free-tailed manakins (*Pipra filicauda*), there is a positive correlation between network position and reproductive success, as central individuals had increased access to preferential mates (Ryder et al. 2008). Furthermore, maintenance of social relationships by yearlings in male long-tailed manakins (*Chiroxiphia linearis*) proved to predict long-term reproductive success in adulthood (McDonald 2007). Alternatively, across many bird taxa, females with larger numbers of connections can increase their reproductive output by copulating with more than one male (McDonald et al. 2013). There is also explicit evidence for increasing reproductive success with increasing connectivity in mammals. For example, female baboons (*Papio cynocephalus*) were noted to maintain network positions that limited agonistic interactions to maximize feeding rates (King et al. 2011) and those with increased social connectivity had higher rates of offspring production (Silk et al. 2009). However, few studies have directly measured the fitness trade-offs of network position for mammals outside of the order Primates (Krause et al. 2007, Krause et al. 2015).

There is also evidence for links between reproductive output, body condition, and sociality. Body condition is a reflection of the ability to acquire and assimilate necessary resources. Individuals that can cooperatively defend a territory and increase foraging time should exhibit better body condition overall, ultimately increasing the likelihood of survival (Lailvaux and Kasumovic 2011, Benson and Bednarz 2010). Across taxa, there is widespread evidence for larger females producing more offspring (Blondel et al. 2002, Du et al. 2005, Swanson et al. 2011). In particular, this has been demonstrated in several sciurid species (Neuhaus 2000, Wauters and Dhondt 1989, 1995). In Columbian ground squirrels (*Urocitellus columbianus*), females are likely to manipulate their litter size during lactation in order to maximize reproductive output after weaning based on maternal body mass, where smaller females are less likely to wean pups than heavier females (Neuhaus 2000). Therefore, these factors are intrinsically related. When considering the impact of sociality on reproductive success, it is imperative that body condition be considered as a covariate to account for this relationship between sociality and body condition.

One common cost to social grouping is intraspecific competition for resources (Table 3.1). Within small group sizes, individuals can cooperatively defend territories to increase foraging success for the group. However, when group sizes become too large or an individual has too many connections to other individuals, the competition for resources can also increase (Scarry 2013). For example, baboons were noted to maintain network positions through a dominance hierarchy that limited agonistic interactions to reduce competition and increase foraging time in order to best exploit their social structure and individual success (King et al. 2011). There is a clear trade-off between access to resources and sharing of those resources within a group, as group size must be optimized for resource acquisition. The result of an increase in competition in large groups could mean increased numbers of aggressive interactions and ultimately dispersal from the group or death from injuries. Dispersal in social species typically occurs during the pre-reproductive stages of life (Clobert 2012). For birds, females will typically leave the group, while for mammals, the males will typically be the dispersing sex (Greenwood 1980, Dobson 1982). The potential costs of dispersal include loss of information transfer from conspecifics, increased predation risk, and ultimately, reduced survival. These costs of dispersal may outweigh the costs of maintaining social connections within a group that is displaying highly agonistic behaviours. For example, the banded mongoose (*Mungos mungo*) is a cooperatively breeding species, that experiences both forced evictions and voluntary dispersals of individuals at intermediate ages from natal groups, generally with a small number of dominant males and females carrying out the largest number of aggressive interactions, encouraging the departures (Cant et al. 2001). For the voluntary dispersals, it appears that finding preferential mates may be a key factor for the dispersal (Cant et al. 2001). The changing social structure of these intermediate age individuals through dispersal may indicate an increase in overall reproductive success, despite the costs of leaving familiar individuals and home ranges.

Black-tailed prairie dogs (*Cynomys ludovicianus*, hereafter 'prairie dogs') are a social, fossorial, herbivorous rodent (Hoogland 1995). Their social structure and associated costs, including infanticide and territorial defense, has been extensively studied (Chapter 2, Hoogland 1995), however, the potential costs and benefits of individual variation in levels of sociality has yet to be explored. Prairie dogs exist in tightly-knit social groupings termed coteries, of approximately six individuals, that work to defend territories, cooperatively breed, and share predator knowledge through alarm calls. As with most social mammal species, typically, females

stay in the natal home range, while males disperse after their first winter (Hoogland 1995). Male dispersal is thought to reduce the amount of inbreeding within the colony and improve fitness (Hoogland 1982). Additionally, it has been shown that prairie dogs will disperse from their coterie when other cooperative kin have died or dispersed (Hoogland 2013), suggesting that a lack of cooperative neighbours promotes dispersal to new areas. Typically, dispersals occur when dominant males are consistently aggressive to yearling males, decreasing the amount of time for foraging and increasing potential injuries where the costs of sociality outweigh the benefits.

During the lactation period of prairie dogs, infanticide by related females is prevalent (Hoogland 1995). Many observations have noted the dynamic switch from female cooperation to territorial disputes and aggressive interactions during this period (Hoogland 1995). In contrast to results from other taxa, that suggest female reproductive success is correlated with increased social connectivity, this may not hold true for prairie dogs due to the risk of infanticide during pre-emergence lactation periods. However, in the period following pup emergence, it has been demonstrated that reproductive females change their degree of sociality to match that of other prairie dogs in order to receive the benefits associated with colonial living, thereby implying that variation in sociality is influenced by benefits during other time periods. Social network analysis provides the ability to explore this drastic change in female behaviour that may best explain the fitness consequences associated with both affiliative and agonistic interactions.

3.1.1 Objectives

This chapter will explore the consequences of individual variation in sociality through the balancing of trade-offs of sociality for optimal fitness. The purpose of this study was to directly quantify the consequences of variation in sociality measured as reproductive success and loss from the network (representing death and/or dispersal) using social network analysis. I hypothesized that both reproductive success and loss from the network would be influenced by sociality as social networks of both affiliative and agonistic behaviours in prairie dogs are temporally variable to reflect specific life history events (Chapter 2). Therefore, I predicted that females during lactation with lower affiliative sociality and increased agonistic sociality would have higher reproductive success by focusing primarily on defense of their litter and maintaining energy stores for lactation through foraging. I also expected that individuals experiencing a high

number of aggressive interactions would be more likely to leave the network, as it is costlier to stay in the coterie through risk of injuries or death. Chapter 2 suggested that increased body condition stabilizes social position for adults across sampling periods within the network. It cannot be delineated if better body condition improves and maintains social standing, or if higher centrality maintains better body condition by increased access to improved forage quality. Therefore, as body condition has also been shown to heavily influence reproductive success in similar sciurid species, incorporating body condition metrics into our study will further explain the relationship between sociality, reproduction, and body condition.

3.2 Methods

3.2.1 Study area

All data was collected from a single colony (Walker) located in Grasslands National Park (49° 3'N, 107° 21'W) during July 2016 (hereafter 'post-emergence') and April 2017 (hereafter 'pre-emergence') through an observational study. There are an estimated 800 adult prairie dogs on the colony (unpublished data). In order to document the social network in detail, I focused on one subsection of the colony. The area of the colony where I focused my study was chosen based on the complete census of this area as part of an ongoing study, where all individuals were correctly identifiable, and the area contained a mix of adults and yearlings of both sexes. This area also contained prairie dogs that were habituated to human presence such that observers were presumed not to affect their natural behaviour.

3.2.2 Data collection

3.2.2.1 Individual measures

In order to properly describe social networks, each prairie dog in the network had to be identifiable for behavioural observations. As part of the ongoing study, individual prairie dogs have been captured and marked in methods previously described (Chapter 2). I tagged individuals with unique alphanumeric tags in each pinna and painted them with a unique symbol on the dorsal pelage using Nyanzol-D to permit individual observation from a distance. When each individual was captured, I recorded their sex, age, and reproductive status. To assess body condition, I used methods previously established in Chapter 2, modified from Schulte-Hostedde et al. (2001). Briefly, body mass and skeletal measurements (zygomatic arch length and right

hind foot length) were recorded. I completed a principal component analysis (PCA) for the skeletal measurements and regressed body mass against PC1. The residuals of this regression served as the index for body condition.

I collected reproductive success data for all identified breeding females in the network. Prairie dogs typically copulate in March, give birth in April, with juveniles emerging in May. I palpated all females that had an open vulva (indicative of estrus) for pregnancy from March to April. I regularly trapped (once per week) those females identified as pregnant until emergence of the litter to identify parturition dates, as well as if a litter was lost during gestation or rearing underground. I recorded the nest burrow location based on trapping location and observation of emergence in the morning. Four to six weeks after parturition, pups emerged from their nest burrow, where I observed them with their nest mates and mother. I used number of emerged pups as a metric for reproductive success.

In order to investigate the loss of individuals from a network, I recorded when individuals were no longer present between sampling events. Individuals were considered absent from the network if they did not appear in the following network sampling period but had been present in the preceding network. Individuals that were no longer found in the sampled area were deemed to have dispersed or died. In some instances, the fate of the individual was not known, and for this reason, dispersal and death were counted together as loss from the network.

3.2.2.2 Social behaviours

Social networks were constructed in methods previously established in Chapter 2. Briefly, I constructed the social network using pair-wise behavioural interactions. I observed these behaviours through binoculars as I sat at a distance from the individuals to limit human disturbance. I recorded the behaviours using all occurrence sampling observation techniques. I recorded both affiliative and agonistic interactions between pair-wise groupings. Affiliative interactions were categorized as encounters with only amicable behaviours. Typically, hostile encounters began with amicable behaviours, but then escalated to chasing or fighting (Hoogland 1995). I ranked the interactions according to the intensity of the interactions, where passive interactions received a low ranking and active interactions received a high ranking (Table 2.2). I placed the social behaviour collected from pair-wise interactions into a matrix using weighed scoring based on Table 2.2.

As the social relationships of the prairie dogs are influenced by their spatial arrangement, I also recorded the home range for each prairie dog within the social network as in Chapter 2 (Viblanc et al. 2016). Briefly, two 20 min focal observations for each animal were collected, where I recorded the activity and location of the activity based on a flagged 15 x 15 m cartesian grid system. This was used to delineate social groupings and spatial groupings. However, these focal observations were only collected in 2017 due to an increase in data collection effort.

3.2.3 Data analysis

I completed all analyses in R (v. 3.4.1, R Core Team 2017). I created models for reproductive success and loss from the network based on methods previously established in Chapter 2. Briefly, I used principal component analysis (PCA) to collapse four metrics of centrality (degree, strength, betweenness centrality, eigenvector centrality) using the igraph package (Csardi and Nepusz 2006). The first principal component (PC1) described the overall sociality of an individual, while the second axis (PC2) represented where an individual exists within the network. A high PC2 value indicated a 'hub' individual that connects coteries together, while a low PC2 value indicated an individual that was well-connected within its own coterie. As in Chapter 2, PC1 and PC2 will be referred to as 'centrality' and 'connectedness,' respectively. These values served as independent variables, while reproductive success and loss from the network were the dependent variables. I ran generalized linear models in package glm2 (Marschner 2011) with additional covariates, described below.

For analyzing loss from the network, I used a binomial distribution as my dependent variable was restricted to presence and absence. I included sex, age, body condition, home range size (for 2017 only), and the principal components (PCs) from Chapter 2 as my covariates for each model. As I did not collect absence data following my final sampling event in 2017 post-emergence, analyses were completed for 2016 post-emergence and 2017 pre-emergence. For reproductive success, I used a Poisson distribution as emerging litters were count data. I excluded females in the yearling age class for this analysis, as the rate of success in yearling breeders is very low (occurred twice over two years), and many yearlings choose not to attempt reproduction in their first year of life. This eliminated the uncertainty of the reasons for unsuccessful litters by yearling females. I included body condition as a covariate along with the PCs from Chapter 2. As in Chapter 2, to account for the non-independence of network data, I

compared the slope estimates of each model in the original data set to 1000 permuted estimates using Welch's t-test. Models that were not significantly different from the randomizations were removed from analysis. Models were compared with the Akaike's Information Criterion (AIC) to find the best fit model.

All procedures followed the Canadian Council on Animal Care guidelines for wildlife and were approved by the University of Saskatchewan Animal Care Committee (AUP 20140042).

3.3 Results

3.3.1 Reproductive success

There were 15 successful litters in the 2017 pre-emergence period, and 4 failed litters across all 19 reproductive adult females. Centrality did not correlate with emergent litter size ($p = 0.64$), but connectedness was negatively correlated ($p = 0.03$) for affiliative interactions (Table 3.2). Females that were not connecting coteries together and interacting only within their own coterie were more likely to have a larger number of juveniles emerge from their nest burrow (Figure 3.1). For both agonistic models, I did not see any effect for centrality ($p = 0.75$) or connectedness ($p = 0.88$) on emergent litter sizes (Table 3.2). Body condition ($p = 0.001$) also significantly impacted the number of emergent pups, where increased body condition was correlated with increased number of pups (Figure 3.2). The best model included both body condition and PC2 to explain the variation in emergent litter sizes.

3.3.2 Loss from the network

In terms of sociality predicting loss from the network, affiliative sociality did not appear to have an effect in post-emergence ($p = 0.83$) or pre-emergence ($p = 0.71$) loss (Table 3.3 and Table 3.4). For the post-emergence period, males were more likely to leave the network than females ($p = 0.04$). Individuals experiencing a high number of agonistic interactions were also more likely to leave the network than individuals with fewer numbers of agonistic interactions ($p = 0.04$) in the pre-emergence period, regardless of sex ($p = 0.97$) (Table 3.5, Figure 3.3).

3.4 Discussion

By studying the variation in levels of sociality, I sought to observe the varying effects on fitness through reproductive success and loss from the network (dispersal/death). I had predicted

that more successful reproductive females would have lower affiliative sociality and increased agonistic sociality, while individuals that had higher agonistic sociality would be more likely to leave the network. I found that reproductive success was not influenced by the overall affiliative sociality of the females, but by which individuals the female interacted with, where interactions with coterie members were more likely to increase the number of emergent pups than interactions with non-coterie members individuals. Agonistic sociality did not appear to influence reproductive success, which was unexpected, but it was a strong predictor for loss from the network.

I found that the number of emergent pups for each litter was not predicted by the number of aggressive interactions experienced by the adult females. Hoogland (1995) suggested that female prairie dogs increase the rate of the aggressive interactions in the pre-emergence period in order to defend their litters from potential infanticide, however, our results suggest this does not appear to impact the success rate of the litters. Viblanc et al. (2016) found similar results to Hoogland (1995), where female Columbian ground squirrels with increased occurrences of displaying aggressive behaviours was positively associated with litter mass and annual fitness. However, this was not the case in my study.

Additionally, the number of affiliative social interactions did not affect emergent litter size, but the 'location' of these interactions within the network was highly predictive. Females that interacted within their own coterie were more likely to have more juveniles emerge from their nest burrows, as compared to females that interacted with individuals outside their own coterie. Potentially, by interacting with only coterie members, females are near-by their own litters and can watch for invading females that are likely to commit infanticide. It may also increase the time females spend lactating, as they are much closer to their litter. However, this greatly reduces their information uptake as they are not interacting outside of their own coterie, a potential trade off of sociality and reproductive success. The females that are connecting coteries, which consequently, have smaller litter sizes or litter failure, may be treating this as a trade-off. They are serving as information channels for their own coterie, but do not realize direct fitness benefits. These females may be experiencing indirect fitness benefits through providing information on predator locations or other incoming females. Alternatively, these females may be increasing their interaction to unfamiliar individuals to increase their own information

exchange and potential areas for forage. It may be that they experienced the litter loss, and then moved within their structure to occupy keystone roles.

Alternatively, females that maintain familiar social structure with their coterie-mates, may be benefitting from reduced dynamic change than those interacting outside of their own coterie. Prairie dog life history suggests that the most changes in the network are occurring during this reproductive period as yearlings are dispersing from the natal home range (Hoogland 1995). In Chapter 2, I determined that body condition correlated with stability of social networks, where individuals in better body condition maintained their social connections, and those in poor body condition had a high number of changes in their social structure. Our results here suggest that better body condition also correlates with increased number of emergent juveniles. The more familiar and stable the social environment is, the more emergent juveniles should be expected.

Maintaining bonds between familiar individuals has proven to increase overall fitness in both mammals and birds (Emery et al. 2007). Stability over time has proven to reduce stress levels, reduce aggression, and increase reproductive success (Cameron et al. 2009, Silk 2007, Zayan 1991). Kohn (2017) suggested that the stability of social relationships by familiarity preferences maintained from the fall period through to the spring correlated with spring reproductive output for female cowbirds (*Molothrus ater*). This stability is especially relevant when there are dynamic group changes as familiar relationships help to maintain some structure.

Furthermore, as lactation is highly energetically costly (Lochmiller et al. 1982), the number of juveniles weaned is indicative of how many resources a female had stored. This energetic cost is particularly important for species that hibernate over the winter (Zervanos et al. 2014), having lost body mass, these individuals are typically at their lowest mass during reproduction. Neuhaus (2000) determined that female Columbian ground squirrels, a hibernating income breeder, modified their litter sizes pre- and post-parturition in response to their body mass, in order to best increase the survival rate of their litter.

Due to the protected status of prairie dog in Canada, I was not able to measure litter size and mass at parturition, as prairie dogs are born underground and it would not have been prudent to have births in a laboratory setting. In instances where this has been performed in related sciurids, female body mass has related to the mass of their litter as well. Indicating that larger females have more income to reproduce at higher rates. Viblanc et al. (2016) were able to

measure litter mass at birth, as the litters were born in a laboratory before being returned to their nest burrows. They found that litter mass was positively correlated with the number of outward defensive interactions of the female (Viblanc et al. 2016).

In terms of evidence for dispersal (or loss from the network), the number of agonistic interactions was positively correlated during the reproductive period. The reproductive period is the time I expected the highest number of changes within the network, and a rapid movement of yearlings between coteries. Continuously encountering aggressive individuals reduces feeding time and increases the likelihood of dispersing to a new area. I did not see an effect of sex on dispersal for the pre-emergence period, when dispersal by yearling males is expected to occur at the higher rate (Hoogland 1995). There is no evidence of male dispersal at higher rates than females in the pre-emergence period in this specific population. What appeared to be a unique dispersal event occurred in 2017, potentially obscuring the observation of typical dispersal movements. In the pre-emergence monitoring period, 24 individuals left the network, 17 of which were found in other locations. These individuals included yearlings and adults of both sexes. This was a much larger dispersal event than expected for the sample area. There appeared to be both natal and breeding dispersal occurring over this period, potentially due to high density and this may have obscured any expected signals for dispersal. Repeating the observations again in future years may find the expected relationship. Lusseau (2003) observed that experimentally removing an individual within a bottlenose dolphin (*Tursiops truncatus*) pod did not change the overall connectedness between other individuals in the network and there did not seem to be an overall effect of loss of one individual. However, their study does not take into account widespread loss events as observed in the prairie dog colony and requires further analysis.

Interestingly, I saw a loss of males between the 2016 post-emergence and 2017 pre-emergence sampling periods, a period that does not typically have sex-based dispersal. It may be possible that these individuals died over winter, or simply dispersed during the late fall or early spring. As the 2016 network had many coteries with two males, it was typically one of these males that left the network before the pre-emergence sampling period. This dispersal may suggest that these males determined that their mating opportunities may be better in other areas due to the presence of other males in their home coterie. Because I did not sample the population continuously between the 2016 post-emergence and 2017 pre-emergence, I cannot surmise if these individuals left the network in the fall before hibernation or if they disappeared in the early

spring after copulation. Both time periods could suggest that optimal mate choice for the following year would be best gained by dispersal. Due to our sampling efforts in past years, I ascertained that these males that dispersed were experiencing their second dispersal event, as they were not dispersing from their natal home range. As Jack and Fedigan (2004) observed in white-faced capuchins (*Cebus capucinus*), this secondary dispersal is typically due to increasing their reproductive opportunities. Further exploration of this secondary dispersal would strengthen this hypothesis as I was not able to relocate all individuals that left the network sampling area.

Overall, SNA was able to explore expected consequences of sociality in black-tailed prairie dogs. I found some expected relationships between body condition and emergence of litters; however, I did not see the expected increase in aggression in females, nor the expected male dominated dispersal in the pre-emergence period. In order to further investigate these patterns found in other populations of prairie dogs, continuing long-term monitoring would be advantageous. This would also allow for investigation of the impact of varying densities of the sample area and changing climatic variables. For example, how a late spring may impact this highly important time for prairie dog success. As well, increasing the sampling effort in other areas of the colony may be able to answer some of the questions related to dispersal/death.

Costs and benefits of sociality have been addressed at the species level and continue to be explored at the individual level. I have surmised that individual variation in sociality can help balance the costs and benefits of these social relationships. By decreasing sociality to within familiar individuals, a female can increase her reproductive success. As well, if an individual is able to maintain consistent social stability, they are more likely to maintain their familiar connections in a dynamic season and likely survival due to access to preferential resources and preferential mates. The main cost of sociality seemed to be driven by competition for mates for males, which is not always the primary source of competition, as resource acquisition becomes more highly contested. Further exploration of trade-offs at an individual level may further reveal the mechanisms of sociality within and between groups.

3.5 Tables

Table 3.1 Summary of trade-offs of centrality for some of the most well-studied taxa in social network analysis.

Trade-offs of centrality	Species	Authors
Benefits		
Increased reproductive success	*Macaca mulatta*	Brent et al. 2011
	Tursiops truncatus	Stanton and Mann 2012
	Polyandrous bird species	McDonald et al. 2013
Increased information exchange	*Ateles geoffroyi*	Ramos-Fernandez et al. 2009
	Tursiops truncatus	Connor 2001
	Paridae	Aplin et al. 2012
	Hymenoptera	Fewell 2003
Increased social cohesion	*Ateles geoffroyi*	Ramos-Fernandez et al. 2009
	Gorilla gorilla gorilla	Stoinski et al. 2003
	Poecilia reticulata	Croft et al. 2009
Increased foraging success	Hymenoptera	Fewell 2003
	Tursiops truncatus	Connor 2001
Costs		
Increased mate competition	*Syncerus caffer*	Krause et al. 2015
Increased disease transmission	*Trichosurus vulpecula*	Corner et al. 2003
	Poecilia reticulata	Croft et al. 2009
Increased resource competition	Many taxa	Krause and Ruxton 2002
Decreased longevity	*Marmota flaviventris*	Blumstein et al. 2018

Table 3.2 Model estimates (± standard error) and significance for generalized linear models predicting number of emergent juveniles per reproductive female black-tailed prairie dog (n = 19) based on metrics of sociality (centrality and connectedness) for the 2017 pre-emergence networks. Bolded metrics indicate significance of $p < 0.05$. Models with lower Akaike's Information Criterion (AIC) are considered better fit than high values.

Network	Factor	Estimate	Std. Error	P value	AIC
Affiliative	Intercept	1.116	0.237	<0.001	86.313
	Centrality	-0.245	0.517	0.635	
	Body condition	**0.005**	**0.002**	**0.003**	
	Intercept	0.935	0.167	<0.001	81.598
	Connectedness	**-2.048**	**0.956**	**0.032**	
	Body condition	**0.003**	**0.001**	**0.043**	
	Intercept	1.026	0.149	<0.001	84.533
	Body condition	**0.004**	**0.001**	**0.001**	
Agonistic	Intercept	1.054	0.173	<0.001	77.657
	Centrality	0.137	0.426	0.747	
	Body condition	**0.006**	**0.002**	**0.001**	
	Intercept	1.029	0.156	<0.001	77.739
	Connectedness	0.052	0.359	0.884	
	Body condition	**0.006**	**0.002**	**0.001**	

Table 3.3 Model estimates (± standard error) and significance for full and final linear models of predicting loss from the network (n = 22) based on metrics of sociality (centrality and connectedness) for the 2016 post-emergence affiliative network in a population of black-tailed prairie dogs. Bolded metrics indicate significance of $p < 0.05$. Models with lower Akaike's Information Criterion (AIC) are considered better fit than high values.

		Full Model AIC: 27.469			**Final model** AIC: 24.25	
Factor	**Estimate**	**Std. Error**	**P value**	**Estimate**	**Std. Error**	**P value**
Intercept	-18.570	3256.000	0.995	-2.576	1.041	0.013
Centrality	-0.261	0.868	0.764	-0.183	0.861	0.832
Sex: Male	**2.425**	**1.624**	**0.135**	**2.586**	**1.263**	**0.041**
Age:Yearling	16.260	3256.000	0.996	Not fit	Not fit	Not fit
Body condition	-0.002	0.007	0.819	Not fit	Not fit	Not fit

		Full Model AIC: 25.66			**Final model** AIC: 22.025	
Factor	**Estimate**	**Std. Error**	**P value**	**Estimate**	**Std. Error**	**P value**
Intercept	-17.860	3065.000	0.995	-2.883	1.195	0.016
Connectedness	-1.815	1.475	0.996	-1.772	1.317	0.178
Sex: Male	2.112	1.548	0.735	2.554	1.362	0.061
Age: Yearling	15.270	3065.000	0.218	Not fit	Not fit	Not fit
Body condition	0.002	0.007	0.172	Not fit	Not fit	Not fit

Table 3.4 Model estimates (± standard error) and significance for full and final linear models of predicting loss from the network based on metrics of sociality (centrality and connectedness) for the 2017 pre-emergence affiliative network (n = 57) in a population of black-tailed prairie dogs. Bolded metrics indicate significance of $p < 0.05$. Models with lower Akaike's Information Criterion (AIC) are considered better fit than high values.

	Full Model AIC: 68.664			**Final model** AIC: 61.544		
Factor	**Estimate**	**Std. Error**	**P value**	**Estimate**	**Std. Error**	**P value**
Intercept	-0.736	0.717	0.305	-0.586	0.323	0.070
Centrality	0.172	0.974	0.860	-0.229	0.615	0.710
Sex: Male	-0.217	0.789	0.784	Not fit	Not fit	Not fit
Age: Yearling	0.662	0.908	0.466	Not fit	Not fit	Not fit
Body condition	-0.001	0.004	0.879	Not fit	Not fit	Not fit
Home range size	-8.768	60.530	0.885	Not fit	Not fit	Not fit

	Full Model AIC: 65.49			**Final model** AIC: 60.391		
Factor	**Estimate**	**Std. Error**	**P value**	**Estimate**	**Std. Error**	**P value**
Intercept	-0.399	0.690	0.563	-0.585	0.3197	0.0673
Connectedness	1.258	0.766	0.101	0.6292	0.5701	0.2698
Sex: Male	-0.317	0.756	0.675	Not fit	Not fit	Not fit
Age: Yearling	0.895	0.751	0.233	Not fit	Not fit	Not fit
Body condition	-0.001	0.004	0.758	Not fit	Not fit	Not fit
Home range size	-67.539	71.839	0.347	Not fit	Not fit	Not fit

Table 3.5 Model estimates (± standard error) and significance for full and final linear models predicting loss from the network based on metrics of sociality (centrality and connectedness) for the 2017 pre-emergence agonistic network (n = 50) in a population of black-tailed prairie dogs. Bolded metrics indicate significance of $p < 0.05$. Models with lower Akaike's Information Criterion (AIC) are considered better fit than high values.

	Full Model AIC: 62.351			**Final model** AIC: 55.889		
Factor	**Estimate**	**Std. Error**	**P value**	**Estimate**	**Std. Error**	**P value**
Intercept	1.000	0.730	0.171	0.4067	0.3066	0.1846
Centrality	**1.985**	**1.087**	**0.068**	**1.8509**	**0.8854**	**0.0366**
Sex: Male	-0.033	0.816	0.968	Not fit	Not fit	Not fit
Age: Yearling	-0.723	0.774	0.350	Not fit	Not fit	Not fit
Body condition	0.001	0.004	0.723	Not fit	Not fit	Not fit
Home range size	2.064	63.169	0.974	Not fit	Not fit	Not fit

	Full Model AIC: 67.663			**Final model** AIC: 60.726		
Factor	**Estimate**	**Std. Error**	**P value**	**Estimate**	**Std. Error**	**P value**
Intercept	-0.693	0.652	0.288	-0.5249	0.3158	0.0965
Connectedness	-0.041	0.631	0.949	0.1087	0.5475	0.8426
Sex: Male	0.641	0.701	0.361	Not fit	Not fit	Not fit
Age: Yearling	-0.167	0.730	0.819	Not fit	Not fit	Not fit
Body condition	0.000	0.004	0.953	Not fit	Not fit	Not fit
Home range size	-11.180	59.860	0.852	Not fit	Not fit	Not fit

3.6 Figures

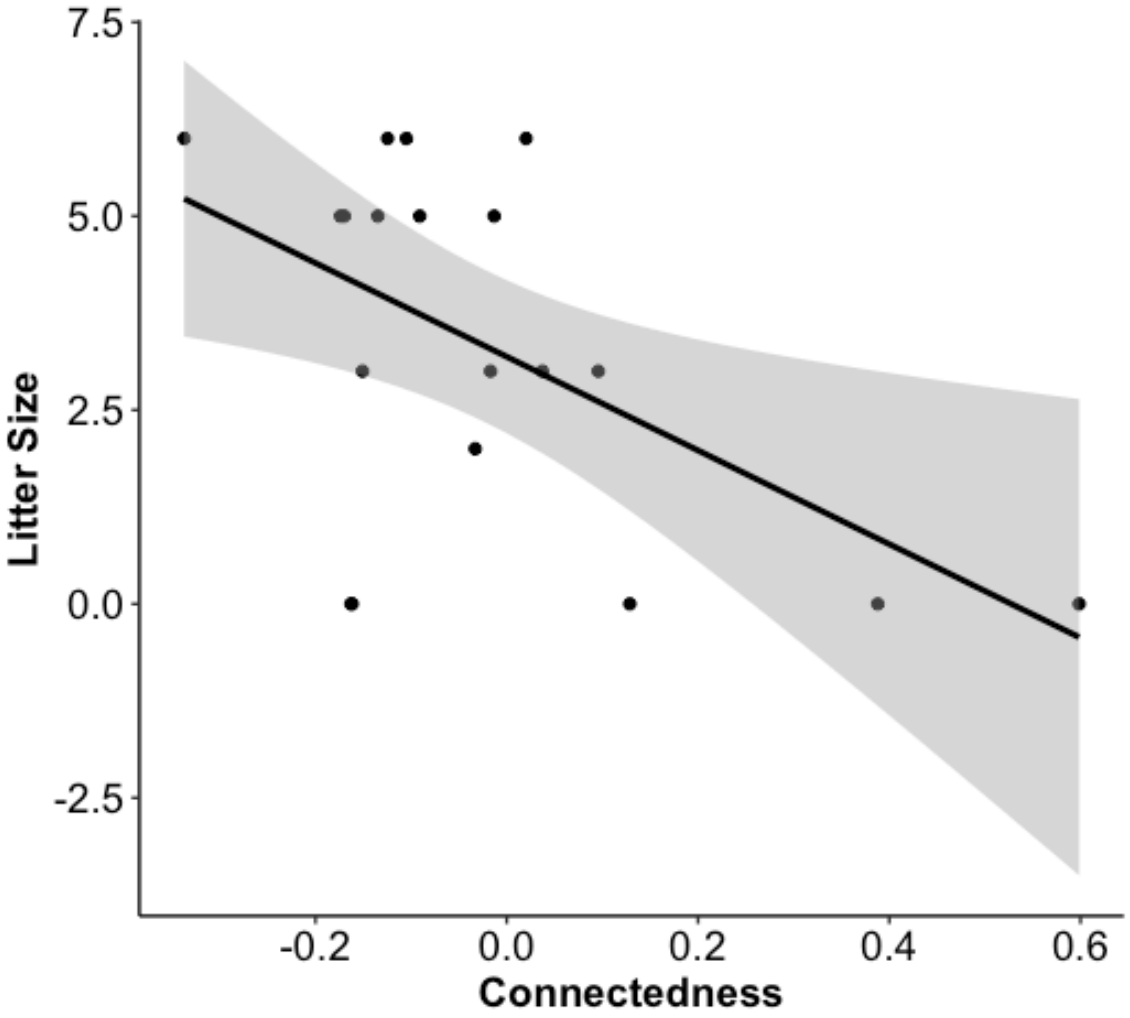

Figure 3.1 The effect of connectedness on number of emergent juveniles per adult female (litter size) for the 2017 pre-emergence affiliative network in black-tailed prairie dogs (n = 19). Grey area represents the 95% confidence interval around the fitted line.

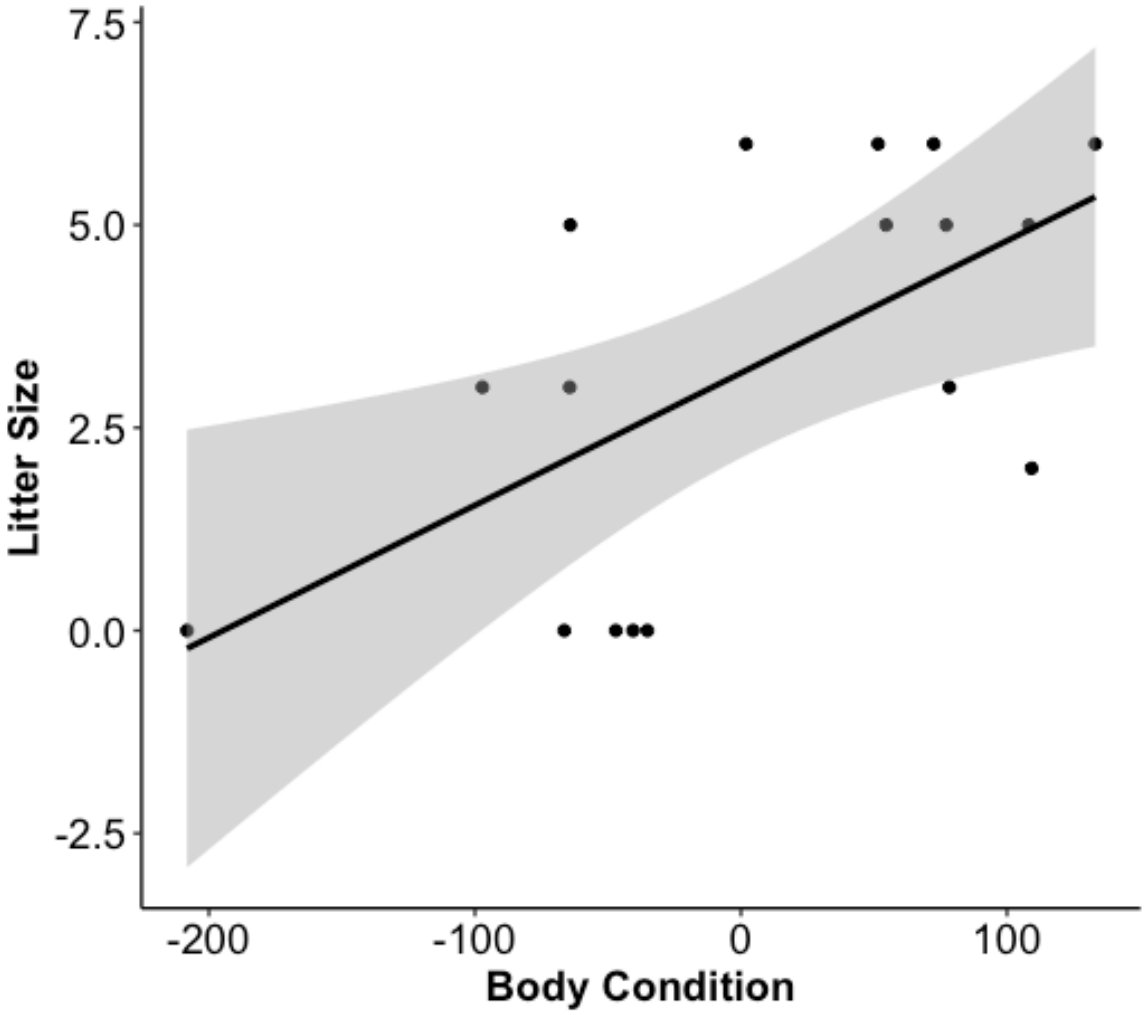

Figure 3.2 The effect of body condition on the number of emergent juveniles per adult female (litter size) for the 2017 pre-emergence affiliative network in black-tailed prairie dogs (n = 19). Grey area represents the 95% confidence intervals around the fitted line.

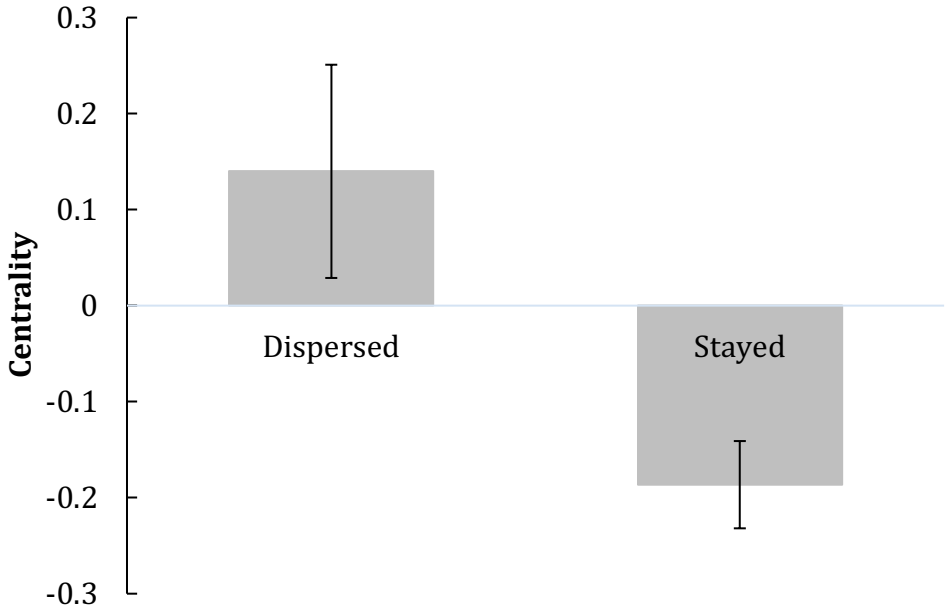

Figure 3.3 The average centrality value for individual black-tailed prairie dogs (n = 35) that were lost from the 2017 pre-emergence agonistic network (represented as dispersed) and those that stayed in the network. Error bars represent standard error.

CHAPTER 4:

GENERAL DISCUSSION

4.1 Social network analysis implications

By comparing social networks across time periods, I was able to look at individual variation in sociality and potential temporal changes. The change in female behaviour during the reproductive timeline also emphasized that sociality produces costs and benefits not only at the species and population level, but at the individual level. Specifically, reproductive females had a dramatic decrease in sociality from the previous post-emergence season to the following pre-emergence season, which was found to be the clearest signal for reproductive success. Additionally, the role of bridging between coteries was found to change between seasons as well, highlighting the importance of time when making social behaviour observations. Even within a social species, there are periods in which asocial activity ranks higher for fitness. This change of roles between individuals helps to address the dynamic nature of an individual's sociality and the resulting effects.

This study is especially novel for exemplifying the ability to change behaviours while maintaining spatial structure. Spatial and social arrangement were highly correlative but there were changes the frequency of social interactions, while the spatial arrangement remained the same. This poses the question of using proximity as a proxy for sociality, given the dynamic changes observed in my research. However, using this proxy is highly dependent on the factors being studied. Silk et al. (2017) used proximity collars to measure transmission rates of bovine tuberculosis in European badgers (*Meles meles*), where disease could be transmitted in both affiliative and agonistic interactions. Therefore, using proximity as a proxy for sociality is context-dependent to the questions being investigated. The within individual variation is a unique aspect of SNA.

4.2 Social stability

The results of my chapters together suggest that social stability is a contributing factor to reproductive success in black-tailed prairie dogs. Chapter 2 revealed that better body condition increases stability in a network through temporal ERGMs. Social roles were most likely to change for individuals in poorer body condition, suggesting that individuals on the periphery of

a coterie are in fact in poorer condition and may be more likely to disperse. Chapter 3 suggested that better body condition increases litter size survival. I also found that litter size was also correlated with increased interactions with familiar individuals as opposed to individuals from adjacent coteries. This correlation suggests social stability is the ultimate cause for increased reproductive success. Specifically, by focussing on body condition in temporal ERGMs, I was able to best showcase how individual variation in sociality is highly correlated with individual success.

Using temporal ERGMS has further been able to show the importance of stability within social networks, and as a novel application in SNA it opens the possibilities for future analyses. Other continuous data may be used in similar ways to explore this stability and instability in biological networks. For example, modelling parasite load with formation and dissolution of edges could infer transmission rates within a population or looking at age in a long-lived species and its effect on influence within the network. This offers new ways to understand stable social bonds, however there are some limitations in ERGMS, requiring both observational data and a complete data set (Silk and Fisher 2017). Using spatio-proximal data and having missing data are both two drawbacks to the ERGM system. My data set was able to work within this set of limitations and therefore, is an excellent model for future studies, looking to investigate similar hypotheses.

4.3 Geographic differences

Studying the impact of individual variation in social networks in a population at the edge of a geographic range provided new insight on how social behaviours may increase in importance with additional stressors of isolation, low-density populations, and harsh climates. The Canadian population of black-tailed prairie dogs provided an ideal study as their unique social structure may greatly contribute to their population viability, which is unseen in other species. In addition, the location of the Canadian population provided a unique opportunity to study the role of behaviour in range limits, which is currently regarded as an important aspect, but few studies have been completed to address it (Gaston 2009). As climate change continues to modify geographic boundaries, studies on behavioural changes at these limits are becoming more relevant.

My analysis revealed that coterie structure is far more variable that previously described. The traditional coterie structure is understood to be determined by the presence of a breeding male that dispersed to the area and the associated breeding females of that natal coterie. Chapter 2 revealed many coteries that lacked breeding individuals, being entirely composed of non-breeding yearlings. These yearlings were typically kin of both sexes. This difference in coterie structure may be in part due to the additional stressors that the northern periphery of the range induces, and the population found at this northern limit, may in fact, be making the best of a bad situation. Or that survival by having looser coterie structures allows for increased information exchange or home range defense by interacting with individuals beyond kin.

In non-hibernating populations, the winter period is an important time for determining social and spatial boundaries (Smith et al. 1973), but this is restricted to spring in northern populations, which may further support the more fluid arrangement of coteries at the northern periphery, given the decreased time period to establish firm coterie boundaries. It may also further establish that pre-emergence periods are likely the most important periods for long-term success in northern populations and this should be considered in management plans.

4. 4 Management implications

The management plan for black-tailed prairie dogs presented by Parks Canada illustrates gaps in the knowledge for prairie dog conservation including the understanding of consequences of sociality (Tuckwell and Everest, 2009). This research may augment the goals of Parks Canada to understand the most effective strategy to conserve black-tailed prairie dogs, as they are currently a threatened species in Canada (COSEWIC, 2011). For example, the potential for successful translocations of animals relies heavily on the knowledge of social structure and the importance of variation within that structure. Shier et al. (2006) demonstrated that prairie dogs that were moved with their family unit were five times more likely to survive than prairie dogs moved with individuals not from their family in translocation efforts. My results may impact the temporal considerations of these translocations, as Shier et al. (2006) completed their study in the spring period, where the most crucial social bonds are being made. In fact, given the importance of this particular point in phenology, translocations in the late summer may increase survival rates as the coteries have been previously determined and familiarity is at its strongest point.

My research may allow conservation managers to better understand the role of social structure in population success as it can be used to model disease mobility and information about predator awareness, which are two key factors in prairie dog survival. Furthermore, as the spring/pre-emergence period has been highlighted as highly consequential to litter success and social stability, management practices would be best to avoid this timing of events. For example, burrow swabbing (for plague detection in fleas) or habitat management would be less impactful at later times in the year, in order to maximize the natural occurrences in the pre-emergence period.

4.5 Future directions

My results open up future questions related to both SNA and prairie dog social behaviour. Given that this study encompasses three sampling periods, in order to validate the stability hypothesis, it would be of interest to establish a long-term study of the sample population to examine evidence of body condition as a social stabilizer and survival. It would also allow for increased markers of reproductive success by examining juvenile over-winter survival rates. As this past year saw a dramatic dispersal event, a long-term study would also provide an opportunity to observe how this event could continue to create impacts for multiple seasons. By increasing these study beyond two years, the life-time social variation within individuals and in-depth social changes could be examined.

Furthermore, as my social networks incorporated a variety of behaviours, creating social networks of only specific behaviours may reveal new interpretations. It may support specific behaviours that are the basis for social cohesion and may be able to account for reciprocity if focussing on directed behaviours. This would create further possibilities of incorporating theoretical SNA into biological systems.

Given that the coterie structure was so different in this area, a latitudinal study of social groupings across the range may also gain insight into the abiotic factors influencing the change in coterie structure. Specifically, using geographic constraints or variation in micro-habitat instead of assigning spatial arrangement based on coterie groupings may reveal more of the dependency of social relationships on the environment at the local scale, and ultimately the geographic range. This specific population also experience hibernation/torpor bouts, unlike most southern populations, which may explain some differences in social arrangement if we can

understand if there is communal or solitary hibernation occurring. Using contact collars over the winter could elucidate the relationship between hibernation patterns and social networks. As my study only included above ground behaviours, using contact collars to measure underground behaviours could be used to validate how well proximity reflects behaviours, and put further support to proximity-based analyses in other species.

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APPENDIX A: PRINCIPAL COMPONENT AND MODEL SUMMARY TABLES

As each social network was different in its network properties, I ran separate models for each of my social networks. The outputs can be found in this appendix. Tables A.1 – A.5 are the outputs from the principal component analyses (PCA) for each social network. I included one sample output of a PCA to show the relative relationship of each of the four centrality metrics (Figure A.1). Tables A.6 – A.10 are summaries for full and final exponential random graph models (ERGMs) for each social network. Tables A.11 – A.15 are the full and final model summaries for linear regressions in each social network. For both ERGMs and linear regressions, Akaike's Information Criterion (AIC) was used to find the most optimal model. Each set of tables followed the same order of networks: 2016 post-emergence, 2017 pre-emergence affiliative, 2017 post-emergence affiliative, 2017 pre-emergence agonistic, and 2017 post-emergence agonistic.

Table A.1 Axes (PC1, PC2) obtained from a principal component analysis describing social network metrics (degree, strength, betweenness centrality, and eigenvector centrality) for affiliative pair-wise interactions in black-tailed prairie dogs in the 2016 post-emergence period (n = 22). The proportion of variance explained by each axis is also presented.

	PC1	**PC2**
Proportion explained	0.71	0.26
Cumulative proportion	0.71	0.97
Scores		
Degree	1.42	0.45
Strength	1.48	0.18
Betweenness centrality	-0.42	1.45
Eigenvector centrality	1.46	-0.17

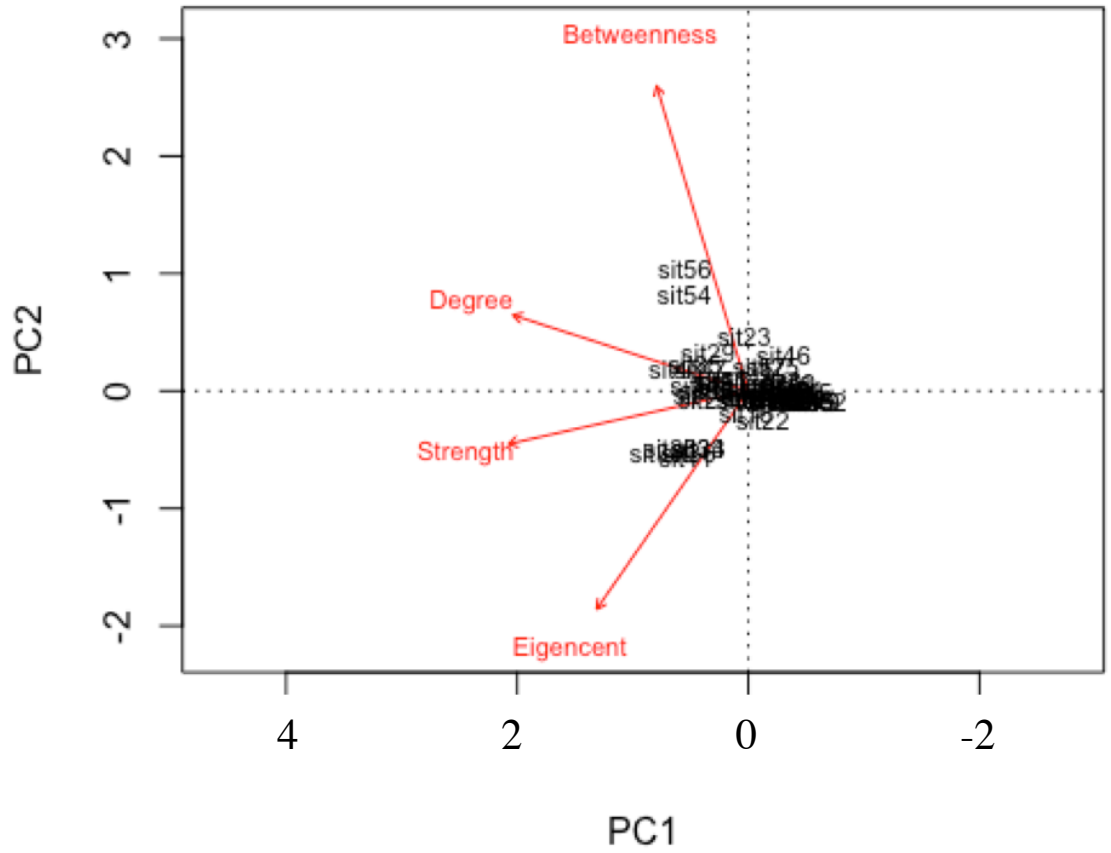

Figure A.1 The results of the principal component analysis for the 2017 pre-emergence affiliative metrics of centrality in black-tailed prairie dogs.

Table A.2 Axes (PC1, PC2) obtained from a principal component analysis describing social network metrics (degree, strength, betweenness centrality, and eigenvector centrality) for affiliative pair-wise interactions in black-tailed prairie dogs in the 2017 pre-emergence period (n = 57). The proportion of variance explained by each axis is also presented.

	PC1	**PC2**
Proportion explained	0.55	0.28
Cumulative proportion	0.55	0.83
Scores		
Degree	1.77	0.4
Strength	1.8	-0.28
Betweenness centrality	0.69	1.62
Eigenvector centrality	1.14	-1.16

Table A.3 Axes (PC1, PC2) obtained from a principal component analysis describing social network metrics (degree, strength, betweenness centrality, and eigenvector centrality) for affiliative pair-wise interactions in black-tailed prairie dogs in the 2017 post-emergence period (n = 36). The proportion of variance explained by each axis is also presented.

	PC1	**PC2**
Proportion explained	0.7	0.18
Cumulative proportion	0.7	0.88
Scores		
Degree	1.5	0.24
Strength	1.58	-0.56
Betweenness centrality	1.18	1.17
Eigenvector centrality	1.43	-0.6

Table A.4 Axes (PC1, PC2) obtained from a principal component analysis describing social network metrics (degree, strength, betweenness centrality, and eigenvector centrality) for agonistic pair-wise interactions in black-tailed prairie dogs in the 2017 pre-emergence period (n = 50). The proportion of variance explained by each axis is also presented.

	PC1	**PC2**
Proportion explained	0.8	0.13
Cumulative proportion	0.8	0.93
Scores		
Degree	1.82	0.28
Strength	1.85	-0.2
Betweenness centrality	1.62	0.88
Eigenvector centrality	1.6	-0.99

Table A.5 Axes (PC1, PC2) obtained from a principal component analysis describing social network metrics (degree, strength, betweenness centrality, and eigenvector centrality) for agonistic pair-wise interactions in black-tailed prairie dogs in the 2017 post-emergence period (n = 13). The proportion of variance explained by each axis is also recorded.

	PC1	**PC2**
Proportion explained	0.75	0.25
Cumulative proportion	0.75	1
Scores		
Degree	1.16	0.61
Strength	1.24	-0.43
Betweenness centrality	1.18	0.58
Eigenvector centrality	0.95	-0.9

Table A.6 Model estimates (± standard error) and significance for the full and final exponential random graph models predicting social homophily in black-tailed prairie dogs (n = 22) in the 2016 post-emergence affiliative network. Bolded metrics indicate significance of $p < 0.05$. Models with lower Akaike's Information Criterion (AIC) are considered better fit than high values.

	Full Model AIC: -363.1			**Final Model** AIC: -363.1		
Metrics	**Estimate**	**Std. Err**	**p-value**	**Estimate**	**Std. Err**	**p-value**
Nonzero	-1.755	0.337	0.001	-1.755	0.337	0.001
Relatedness	**-1.195**	**0.429**	**0.006**	**-1.195**	**0.429**	**0.006**
Distance	**-0.044**	**0.006**	**<0.001**	**-0.044**	**0.006**	**<0.001**
Sex	**0.479**	**0.142**	**0.001**	**0.479**	**0.142**	**0.001**
Age	**1.176**	**0.134**	**<0.001**	**1.176**	**0.134**	**<0.001**
Body condition	**0.003**	**0.000**	**<0.001**	**0.003**	**0.000**	**<0.001**

Table A.7 Model estimates (± standard error) and significance for the full and final exponential random graph models predicting social homophily in black-tailed prairie dogs (n = 57) in the 2017 pre-emergence affiliative network. Bolded metrics indicate significance of $p < 0.05$. Models with lower Akaike's Information Criterion (AIC) are considered better fit than high values.

	Full Model AIC: -2517			**Final Model** AIC: -2519		
Metrics	**Estimate**	**Std. Err**	**p-value**	**Estimate**	**Std. Err**	**p-value**
Nonzero	-4.033	0.150	<0.001	-4.016	0.157	<0.001
Relatedness	0.128	0.154	0.406	Not fit	Not fit	Not fit
Distance	**-0.004**	**0.001**	**<0.001**	**-0.004**	**0.001**	**<0.001**
Sex	0.076	0.053	0.153	Not fit	Not fit	Not fit
Age	**1.313**	**0.051**	**<0.001**	**0.348**	**0.045**	**<0.001**
Body condition	0.000	0.000	0.505	Not fit	Not fit	Not fit

Table A.8 Model estimates (± standard error) and significance for the full and final exponential random graph models predicting social homophily in black-tailed prairie dogs (n = 36) in the 2017 post-emergence affiliative network. Bolded metrics indicate significance of $p < 0.05$. Models with lower Akaike's Information Criterion (AIC) are considered better fit than high values.

	Full Model AIC: -984.9			**Final Model** AIC: -989.7		
Metrics	**Estimate**	**Std. Err**	**p-value**	**Estimate**	**Std. Err**	**p-value**
Nonzero	-3.276	0.266	<0.001	-3.282	0.266	<0.001
Relatedness	**0.840**	**0.291**	**0.004**	**0.895**	**0.262**	**0.001**
Distance	**-0.011**	**0.002**	**<0.001**	**-0.011**	**0.002**	**<0.001**
Sex	0.031	0.114	0.787	Not fit	Not fit	Not fit
Age	**1.206**	**0.098**	**<0.001**	**1.210**	**0.094**	**<0.001**
Body condition	0.000	0.000	0.398	Not fit	Not fit	Not fit

Table A.9 Model estimates (± standard error) and significance for the full and final exponential random graph models predicting social homophily in black-tailed prairie dogs (n = 50) in the 2017 pre-emergence agonistic network. Bolded metrics indicate significance of $p < 0.05$. Models with lower Akaike's Information Criterion (AIC) are considered better fit than high values.

	Full Model AIC: -1866			**Final Model** AIC: -1870		
Metrics	**Estimate**	**Std. Err**	**p-value**	**Estimate**	**Std. Err**	**p-value**
Nonzero	-4.101	0.200	<0.001	-4.072	0.200	<0.001
Relatedness	0.349	0.310	0.260	Not fit	Not fit	Not fit
Distance	**-0.003**	**0.002**	**0.038**	**-0.004**	**0.001**	**0.015**
Sex	**0.395**	**0.100**	**<0.001**	**0.423**	**0.103**	**<0.001**
Age	**0.283**	**0.096**	**0.003**	**0.291**	**0.104**	**0.005**
Body condition	**0.002**	**0.001**	**0.001**	**0.002**	**0.001**	**0.001**

Table A.10 Model estimates (± standard error) and significance for the full and final exponential random graph models predicting social homophily in black-tailed prairie dogs (n = 13) in the 2017 post-emergence agonistic network. Bolded metrics indicate significance of $p < 0.05$. Models with lower Akaike's Information Criterion (AIC) are considered better fit than high values.

	Full Model AIC: -93.60			**Final Model** AIC: -95.26		
Metrics	**Estimate**	**Std. Err**	**p-value**	**Estimate**	**Std. Err**	**p-value**
Nonzero	-2.084	0.666	0.003	-2.491	0.606	<0.001
Relatedness	-0.013	2.300	0.995	Not fit	Not fit	Not fit
Distance	-0.021	0.011	0.056	-0.018	0.009	0.057
Sex	**1.000**	**0.326**	**0.003**	**0.995**	**0.289**	**0.001**
Age	-1.026	0.785	0.195	Not fit	Not fit	Not fit
Body condition	0.001	0.002	0.535	Not fit	Not fit	Not fit

Table A.11 Model estimates (± standard error) and significance for full and final linear models of predicting centrality and connectedness for the 2016 post-emergence affiliative network (n = 22) in a population of black-tailed prairie dogs. Bolded metrics indicate significance of p<0.05. Models with lower Akaike's Information Criterion (AIC) are considered better fit than high values.

		Full Model			**Final model**		
		F(16) = 1.69 p = 0.19 AIC = 47.86			F(20) = 2.79 p = 0.11 AIC = 46.29		
Metric	**Factor**	**Estimate**	**Std. Error**	**P value**	**Estimate**	**Std. Error**	**P value**
Centrality	Intercept	-0.62	0.456	0.326	-0.673	0.425	0.129
	Non-reproductive female	-0.026	0.356	0.943	Not fit	Not fit	Not fit
	Non-reproductive male	-0.363	0.366	0.336	Not fit	Not fit	Not fit
	Body condition	0.001	0.001	0.422	Not fit	Not fit	Not fit
	Coterie size	0.078	0.061	0.216	0.673	0.061	0.11

		Full Model			**Final model**		
		F(16) = 1.80 p = 0.17 AIC = 47.37			F(17) = 1.98 p = 0.14 AIC = 46.75		
Metric	**Factor**	**Estimate**	**Std. Error**	**P value**	**Estimate**	**Std. Error**	**P value**
Connectedness	Intercept	0.088	0.451	0.848	0.025	0.447	0.955
	Non-reproductive female	**-0.680**	**0.352**	**0.072**	**-0.766**	**0.342**	**0.039**
	Non-reproductive male	**-0.912**	**0.363**	**0.023**	**-0.843**	**0.357**	**0.03**
	Body condition	0.001	0.001	0.324	Not fit	Not fit	Not fit
	Coterie size	0.078	0.060	0.216	0.088	0.059	0.154

Table A.12 Model estimates (± standard error) and significance for full and final linear models predicting centrality and connectedness for the 2017 pre-emergence affiliative network (n = 57) in a population of black-tailed prairie dogs. Bolded metrics indicate significance of p<0.05. Models with lower Akaike's Information Criterion (AIC) are considered better fit than high values.

		Full Model			**Final model**		
		F(37) = 11.06 p < 0.001 AIC = 46.57			F(42) = 18.69 p < 0.001 AIC = 37.63		
Metric	**Factor**	**Estimate**	**Std. Error**	**P value**	**Estimate**	**Std. Error**	**P value**
Centrality	Intercept	-0.307	0.153	0.05	-0.309	0.102	0.004
	Non-reproductive female	**0.725**	**0.163**	**<0.001**	**-0.724**	**0.130**	**<0.001**
	Non-reproductive male	**0.954**	**0.184**	**<0.001**	**-0.925**	**0.149**	**<0.001**
	Reproductive male	**0.498**	**0.170**	**0.006**	**-0.498**	**0.167**	**0.004**
	Body condition	**0.001**	**0.001**	**0.146**	**0.001**	**0.001**	**0.015**
	Home range	-10.248	8.399	0.229	Not fit	Not fit	Not fit
	Coterie size	0.000	0.020	0.990	Not fit	Not fit	Not fit

		Full Model			**Final model**		
		F(35) = 5.708 p < 0.001 AIC = 69.65			F(40) = 5.11 p < 0.001 AIC = 42.91		
Metric	**Factor**	**Estimate**	**Std. Error**	**P value**	**Estimate**	**Std. Error**	**P value**
Connectedness	Intercept	-0.264	0.150	0.084	-0.496	0.153	0.002
	Non-reproductive female	0.051	0.198	0.796	-0.027	0.200	0.893
	Non-reproductive male	-0.394	0.251	0.124	-0.261	0.219	0.239
	Reproductive male	**0.339**	**0.207**	**0.110**	**0.670**	**0.252**	**0.011**
	Body condition	0.000	0.001	0.790	Not fit	Not fit	Not fit
	Home range	**36.085**	**11.032**	**0.002**	**24.051**	**8.550**	**0.008**
	Coterie size	**0.055**	**0.020**	**0.008**	**0.057**	**0.020**	**0.006**

Table A.13 Model estimates (± standard error) and significance for full and final linear models predicting centrality and connectedness for the 2017 post-emergence affiliative network (n = 36) in a population of black-tailed prairie dogs. Bolded metrics indicate significance of $p < 0.05$. Models with lower Akaike's Information Criterion (AIC) are considered better fit than high values.

		Full Model			**Final model**		
		F(24) = 0.71 p = 0.64 AIC = 64.23			F(29) = 3.78 p = 0.08 AIC = 55.91		
Metric	**Factor**	**Estimate**	**Std. Error**	**P value**	**Estimate**	**Std. Error**	**P value**
Centrality	Intercept	0.147	0.321	0.651	0.280	0.146	0.065
	Non-reproductive female	0.372	0.353	0.303	Not fit	Not fit	Not fit
	Non-reproductive male	0.402	0.425	0.353	Not fit	Not fit	Not fit
	Reproductive male	0.106	0.374	0.780	Not fit	Not fit	Not fit
	Body condition	0.001	0.001	0.666	Not fit	Not fit	Not fit
	Home range	-7.525	11.055	0.503	-13.490	7.341	0.077
	Coterie size	-0.020	0.044	0.657	Not fit	Not fit	Not fit

		Full Model			**Final model**		
		F(24) = 0.91 p = 0.50 AIC = 67.64			F(34) = 4.73 p = 0.04 AIC = 63.42		
		Estimate	**Std. Error**	**P value**	**Estimate**	**Std. Error**	**P value**
Connectedness	Intercept	-0.443	0.340	0.204	-0.423	0.215	0.058
	Non-reproductive female	-0.181	0.373	0.631	Not fit	Not fit	Not fit
	Non-reproductive male	-0.322	0.449	0.481	Not fit	Not fit	Not fit
	Reproductive male	-0.178	0.395	0.656	Not fit	Not fit	Not fit
	Body condition	0.000	0.001	0.743	Not fit	Not fit	Not fit
	Home range	3.273	11.680	0.782	Not fit	Not fit	Not fit
	Coterie size	**0.081**	**0.047**	**0.096**	**0.06403**	**0.02944**	**0.037**

Table A.14 Model estimates (± standard error) and significance for full and final linear models predicting centrality and connectedness for the 2017 pre-emergence agonistic network (n = 50) in a population of black-tailed prairie dogs. Bolded metrics indicate significance of p<0.05. Models with lower Akaike's Information Criterion (AIC) are considered better fit than high values.

		Full Model			**Final model**		
		F(36) = 4.03 p = 0.003 AIC = 65.22			F(39) = 6.859 p < 0.001 AIC = 63.08		
Metric	**Factor**	**Estimate**	**Std. Error**	**P value**	**Estimate**	**Std. Error**	**P value**
Centrality	Intercept	0.040	0.202	0.843	-0.170	0.111	0.134
	Non-reproductive female	0.395	0.222	0.084	0.310	0.180	0.093
	Non-reproductive male	0.148	0.244	0.549	0.002	0.200	0.990
	Reproductive male	**0.988**	**0.240**	**<0.001**	**0.953**	**0.222**	**<0.001**
	Body condition	-0.001	0.001	0.303	Not fit	Not fit	Not fit
	Home range	-5.810	13.803	0.676	Not fit	Not fit	Not fit
	Coterie size	-0.030	0.027	0.269	Not fit	Not fit	Not fit

		Full Model			**Final model**		
		F(36) = 1.72 p = 0.14 AIC = 79.44			F(46) = 7.80 p = 0.01 AIC = 76.73		
		Estimate	**Std. Error**	**P value**	**Estimate**	**Std. Error**	**P value**
Connectedness	Intercept	0.045	0.238	0.853	-0.002	0.075	0.983
	Non-reproductive female	-0.105	0.262	0.691	Not fit	Not fit	Not fit
	Non-reproductive male	-0.070	0.288	0.809	Not fit	Not fit	Not fit
	Reproductive male	0.272	0.283	0.343	Not fit	Not fit	Not fit
	Body condition	**0.002**	**0.001**	**0.021**	**0.002**	**0.001**	**0.008**
	Home range	-0.153	16.285	0.993	Not fit	Not fit	Not fit
	Coterie size	0.010	0.031	0.751	Not fit	Not fit	Not fit

Table A.15 Model estimates (± standard error) and significance for full and final linear models predicting centrality and connectedness for the 2017 post-emergence Agonistic network (n = 13) in a population of black-tailed prairie dogs. Bolded metrics indicate significance of p<0.05. Models with lower Akaike's Information Criterion (AIC) are considered better fit than high values.

		Full Model F(6) = 1.78 p = 0.25 AIC = 31.43			**Final model** F(11) = 6.06 p = 0.03 AIC = 29.01		
		Estimate	**Std. Error**	**P value**	**Estimate**	**Std. Error**	**P value**
Centrality	Intercept	-0.136	1.577	0.934	-0.563	0.289	0.077
	Non-reproductive female	1.309	1.354	0.371	Not fit	Not fit	Not fit
	Non-reproductive male	1.586	1.292	0.266	Not fit	Not fit	Not fit
	Reproductive male	1.542	0.822	0.110	Not fit	Not fit	Not fit
	Body condition	0.004	0.002	0.166	Not fit	Not fit	Not fit
	Home range	**29.123**	**44.986**	**0.541**	**60.831**	**24.713**	**0.032**
	Coterie size	0.264	0.399	0.533	Not fit	Not fit	Not fit

		Full Model F(6)=5.54 p = 0.03 AIC = 34.16			**Final model** F(11) = 9.88 p = 0.009 AIC = 26.38		
		Estimate	**Std. Error**	**P value**	**Estimate**	**Std. Error**	**P value**
Connectedness	Intercept	-1.866	1.027	0.119	-0.650	0.261	0.030
	Non-reproductive female	-0.302	0.459	0.529	Not fit	Not fit	Not fit
	Non-reproductive male	-0.615	0.505	0.258	Not fit	Not fit	Not fit
	Reproductive male	-0.638	0.593	0.313	Not fit	Not fit	Not fit
	Body condition	0.001	0.001	0.673	Not fit	Not fit	Not fit
	Home range	**99.353**	**29.306**	**0.015**	**70.215**	**22.337**	**0.009**
	Coterie size	0.504	0.260	0.101	Not fit	Not fit	Not fit

APPENDIX B: SOCIAL NETWORK FIGURES

Social network figures created in Gephi (v. 0.9.1, Bastian et al. 2009).

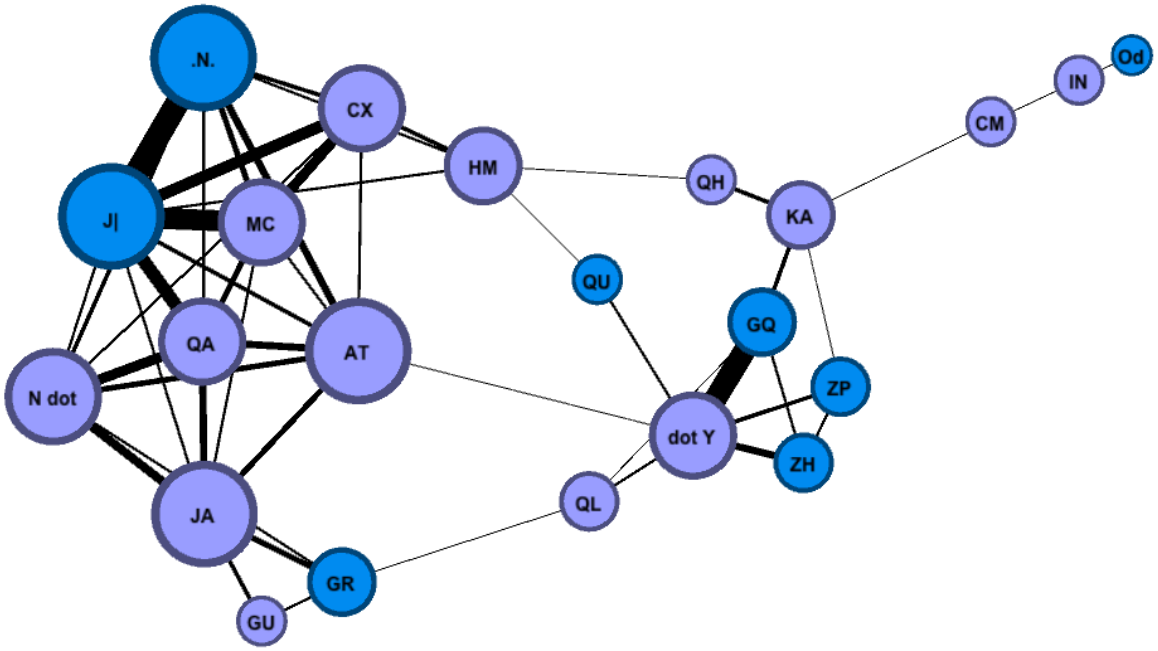

Figure B.1 Social network for affiliative social interactions in the 2016 post-emergence period for 22 individuals. The circles represent each individual, and lines between individuals represent interactions. Larger circles represent individuals with higher degree values. Blue circles represent males, while purple circles represent females. Thicker lines indicate more intense and more frequent interactions.

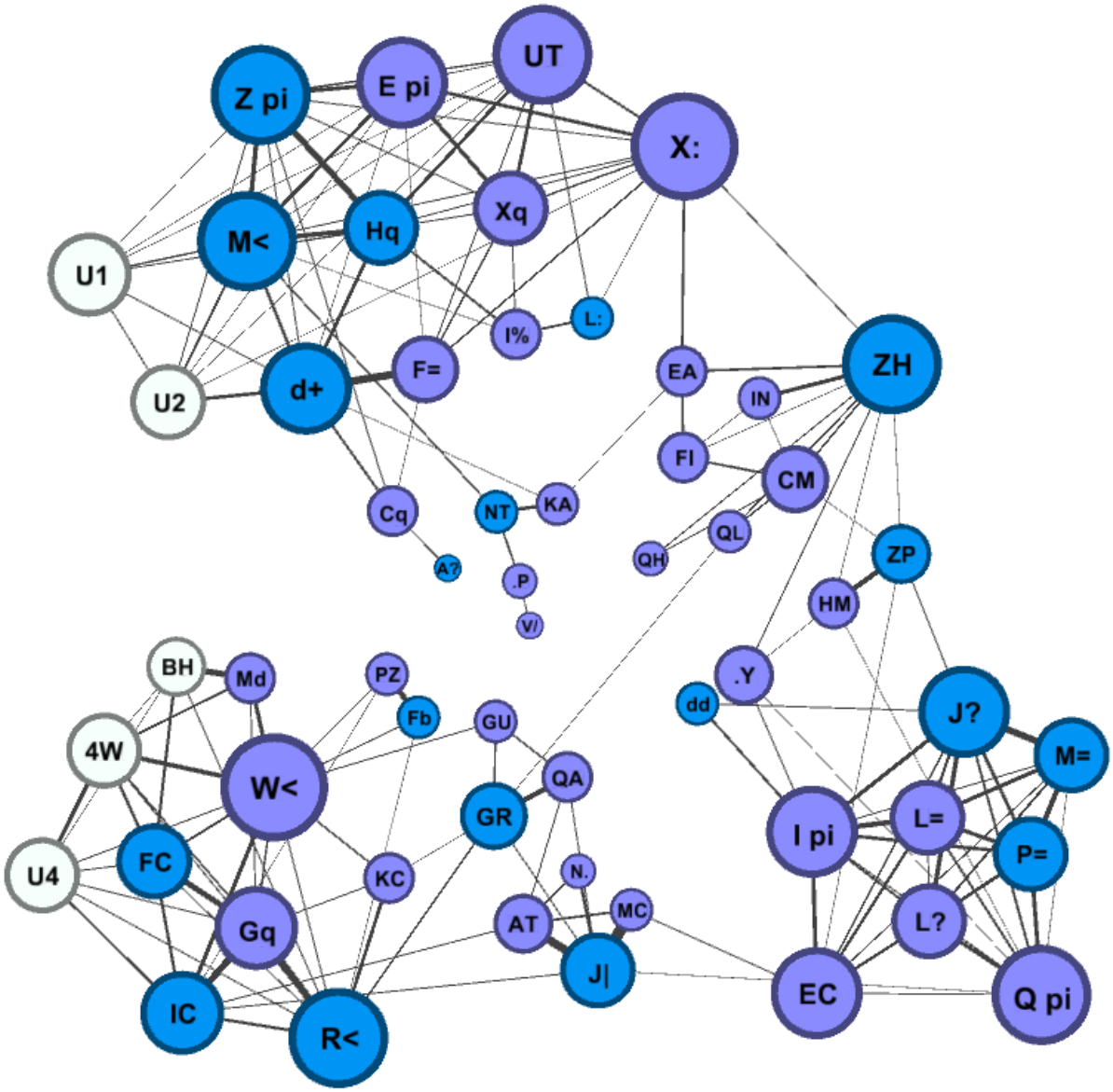

Figure B.2 Social network for affiliative social interactions in the 2017 pre-emergence period for 57 individuals. The circles represent each individual, and lines between individuals represent interactions. Larger circles represent individuals with higher degree values. Blue circles represent males, purple circles represent females, and white circles represent unknown sex. Thicker lines indicate more intense and more frequent interactions.

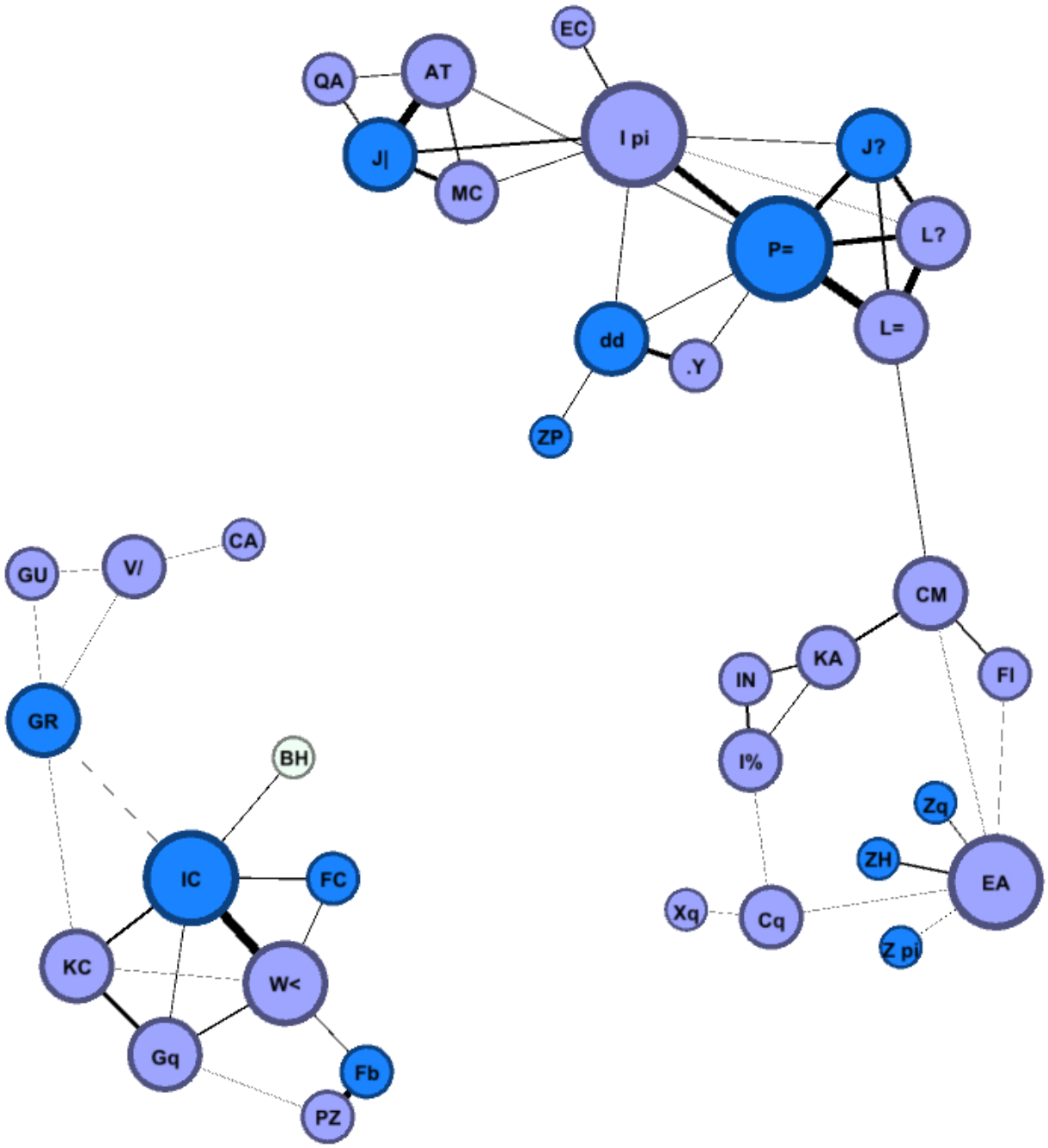

Figure B.3 Social network for affiliative social interactions in the 2017 post-emergence period for 36 individuals. The circles represent each individual, and lines between individuals represent interactions. Larger circles represent individuals with higher degree values. Blue circles represent males, purple circles represent females, and white circles represent unknown sex. Thicker lines indicate more intense and more frequent interactions.

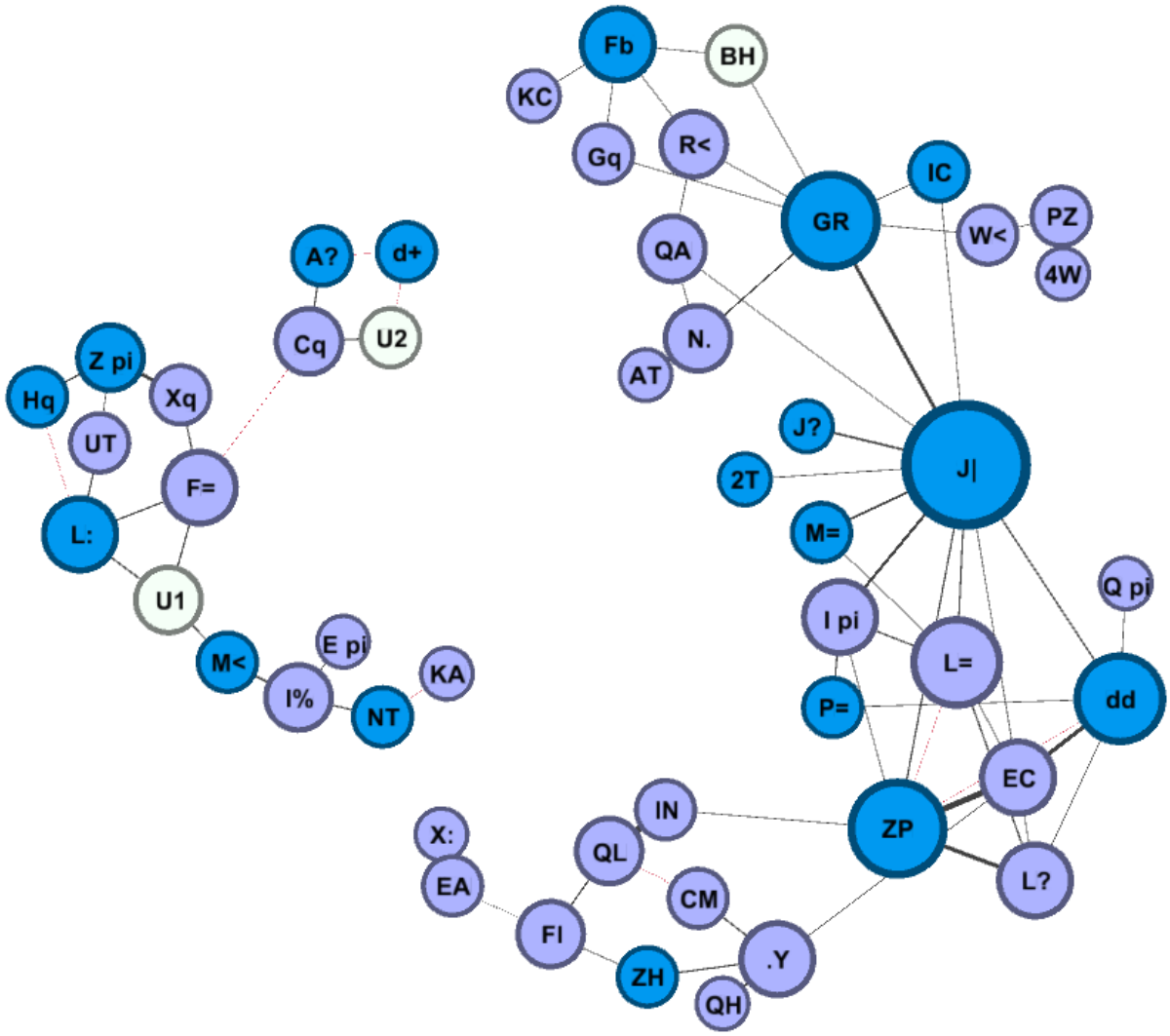

Figure B.4 Social network for agonistic social interactions for the 2017 pre-emergence period for 50 individuals. The circles represent each individual, and lines between individuals represent interactions. Larger circles represent individuals with higher degree values. Blue circles represent males, purple circles represent females, and white circles represent unknown sex. Thicker lines indicate more intense and more frequent interactions.

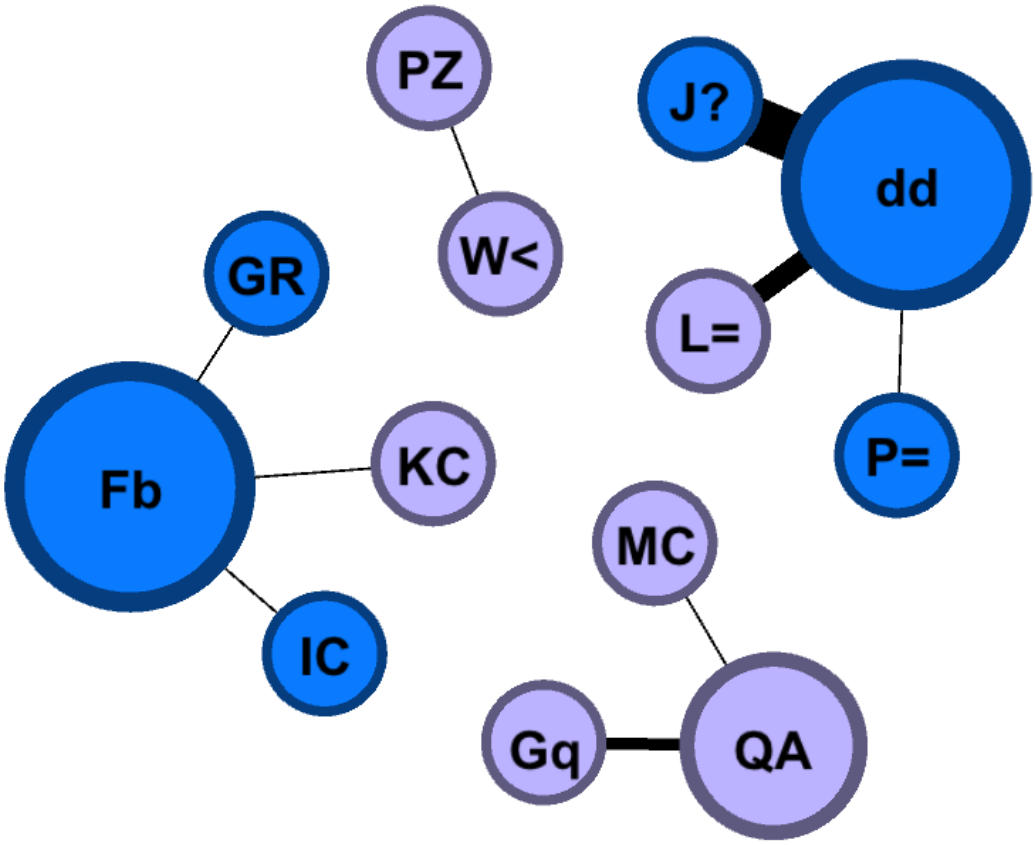

Figure B.5 Social network for agonistic social interactions in the 2017 post-emergence period for 13 individuals. The circles represent each individual, and lines between individuals represent interactions. Larger circles represent individuals with higher degree values. Blue circles represent males, while purple circles represent females. Thicker lines indicate more intense and more frequent interactions.

APPENDIX C: RATES OF BEHAVIOUR

The rates and types of behaviours exhibited by each age and sex class were different between sampling periods. I have presented here a breakdown of the behaviours used, corrected per individual over the sampling period.

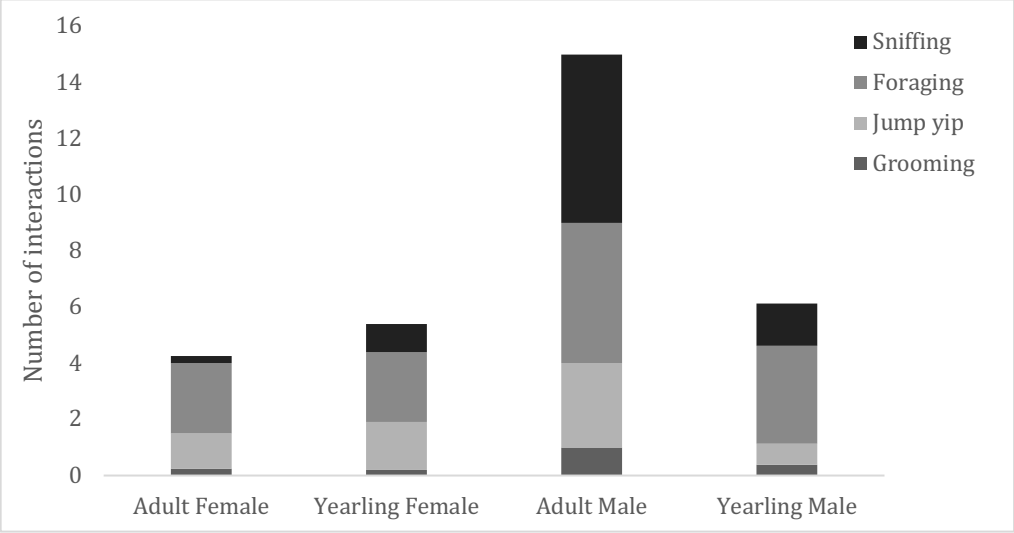

Figure C.1 Affiliative behaviours of black-tailed prairie dogs (n = 22) for the 2016 post-emergence network broken down by sex and age. Behaviour rates are presented as number of interactions per individual.

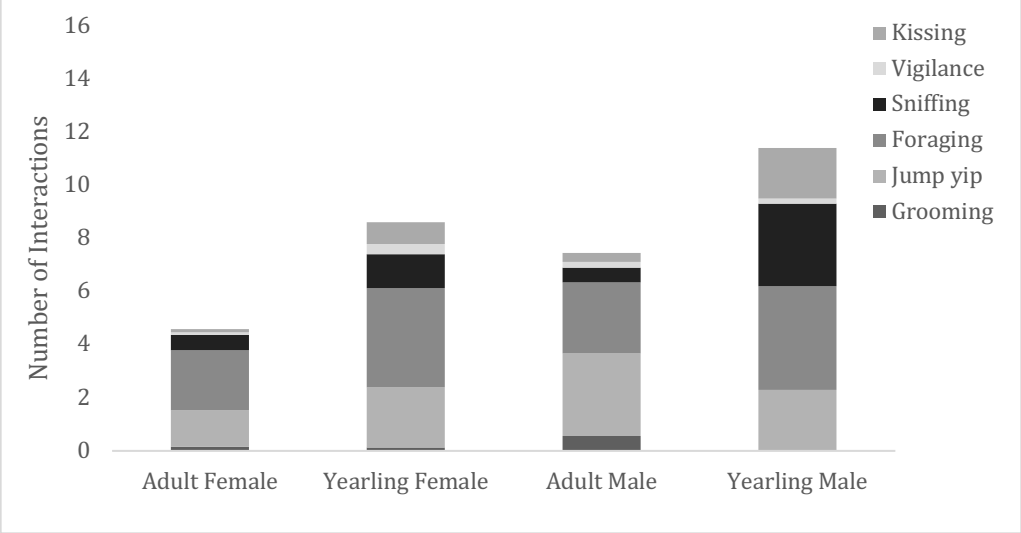

Figure C.2 Affiliative behaviours of black-tailed prairie dogs (n = 57) for the 2017 pre-emergence network broken down by sex and age. Behaviour rates are presented as number of interactions per individual.

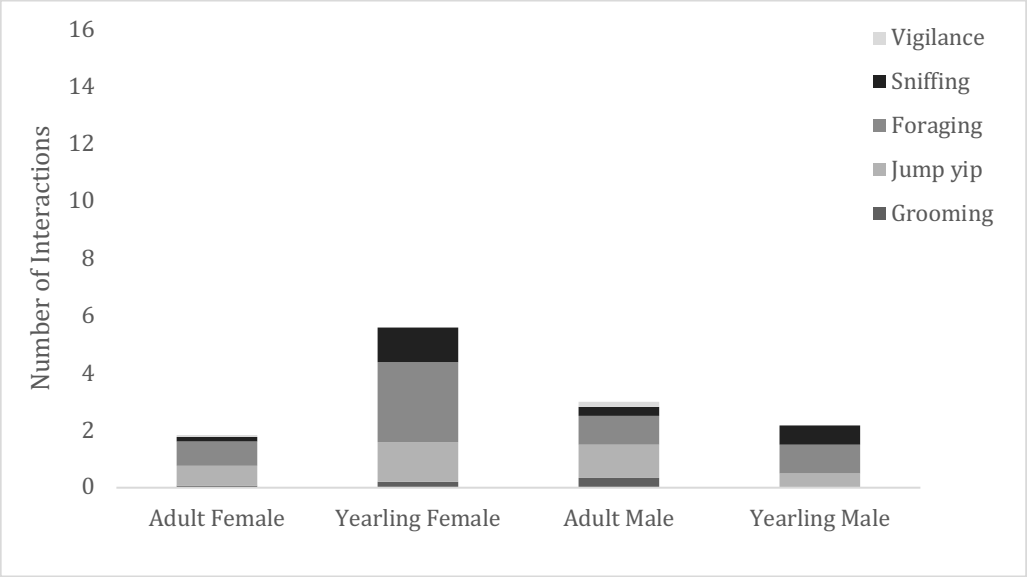

Figure C.3 Affiliative behaviours of black-tailed prairie dogs (n = 36) for the 2017 post-emergence network broken down by sex and age. Behaviour rates are presented as number of interactions per individual.

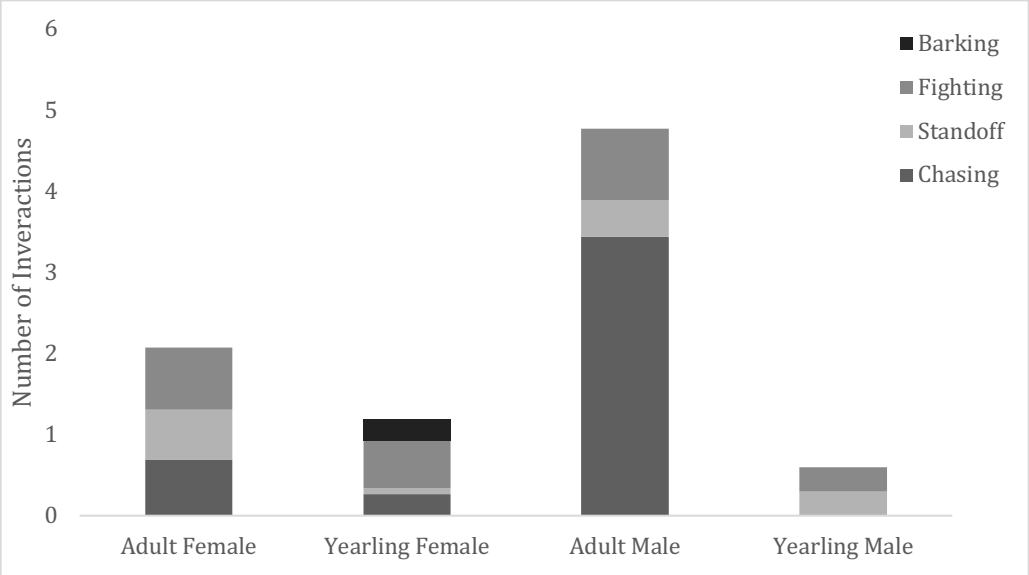

Figure C.4 Agonistic behaviours of black-tailed prairie dogs (n = 50) for the 2017 pre-emergence network broken down by sex and age. Behaviour rates are presented as number of interactions per individual.

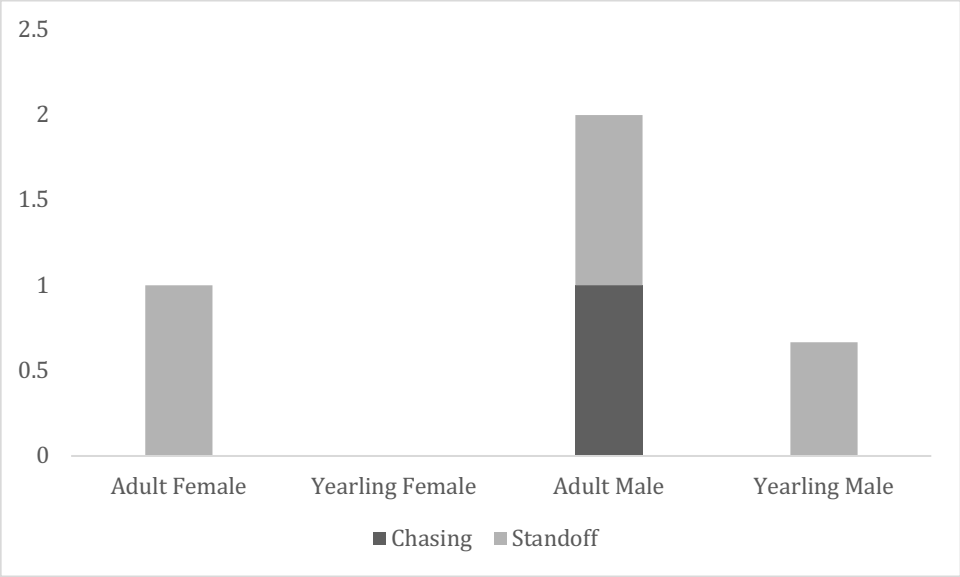

Figure C.5 Agonistic behaviours of black-tailed prairie dogs (n = 13) for the 2017 post-emergence network broken down by sex and age. Behaviour rates are presented as number of interactions per individual.